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Some Middle Pennsylvanian Hoplocarida (Crustacea) and Their Phylogenetic Significance

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INTRODUCTION

Richardson (1956) and Johnson and Richardson (1966, 1968, 1969) have described aspects of the Middle Pennsylvanian Mazon Creek faunas of Illinois. In this paper some new Middle Pennsylvanian hoplocarids from the Essex fauna and the Mecca fauna (Zangerl and Richardson, 1963) are described and their phylogenetic significance evaluated.

The fossil record of the superorder Hoplocarida had, until recently, been confined to representatives of the order Stomatopoda. The Sculidae (*Sculda* Munster, 1840 and *Pseudosculda* Dames, 1886) are known from the Jurassic and Cretaceous, the Squillidae from the Cretaceous to the present. The range of the Gonodactylidae was recently extended back from the Middle Miocene to the Middle Cretaceous with *Paleosquilla brevicoxa* Schram, 1968. Berry (1939) provides a concise review of fossil stomatopods.

In 1962 Brooks erected a new order, the Palaeostomatopoda, which he placed at that time in the extinct superorder Eocarida. The members of this late Palaeozoic order have had a varied taxonomic history. *Archaeocaris* Meek, 1872 was originally compared with the Cumacea. Ortmann (1897) placed this genus in with the Mysidacea. *Perimecturus* Peach, 1908 was first allied with the mysids. Subsequent to his initial observations, Brooks (1969) has re-studied the European material concluding that the Palaeostomatopoda are in fact hoplocarids and that they represent, if not the ancestral stock of the stomatopods, closely related derivatives of it.

The fossil stomatopods known until now did not express any significant deviation from the living forms. With the possible exception of *Paleosquilla*, none displays any really primitive characters. One of

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the new Essex forms, however, provides a morphological link between the palaeostomatopods and the later stomatopods. The range of the extant order is thus moved back from the Jurassic into the Pennsylvanian.

Two of the hoplocarids to be described in this paper cannot be placed in either of the two recognized orders of the Hoplocarida. They possess the typical hoplocarid characteristics: large abdomen, short thorax, articulated rostrum, triramous first antennae, three-jointed thoracic protopods, and abdominal gills. The carapace of these new forms, however, covers the entire thorax and the thoracic legs are unmodified. The assignment of these species to a new order entails modification of our concepts of what constitutes a hoplocarid, a stomatopod, and a palaeostomatopod. The definitions of taxonomic categories will be given as the new material is presented.

In the following descriptions references are made to specific specimens. Prefixes denote the collections in which they are to be found.

PE—Field Museum of Natural History

H—Private collection of Mr. Jerry Herdina, Berwyn, Illinois

HTP—Private collection of Mr. and Mrs. Ted Piecko, Chicago, Illinois

USNM—United States National Museum

W—Private collection of Mr. and Mrs. F. A. Wolff, Park Forest, Illinois

SYSTEMATICS

Superorder: **Hoplocarida** Calman, 1904

Abdomen enlarged; thorax shortened; first antenna with three flagella; rostrum movably articulated to the carapace; protopods of the thoracopods primitively with three segments: preoxa, coxa, and basis; gills on the abdominal appendages; possibly a cephalic kinesis between the first and second antennae. *Miss.-Rec.*

Order: **Aeschronectida** new

Carapace, covering the whole thorax, with a strong development of the lateral wings; thoracic appendages primitively unmodified as chelae or subchelae; thoracopodal inner branch with four segments: ischio-merus, carpus, propodus, and dactylus. (These terms are used in accordance with current anatomical practice and do not imply homology.) *M. Penn.*

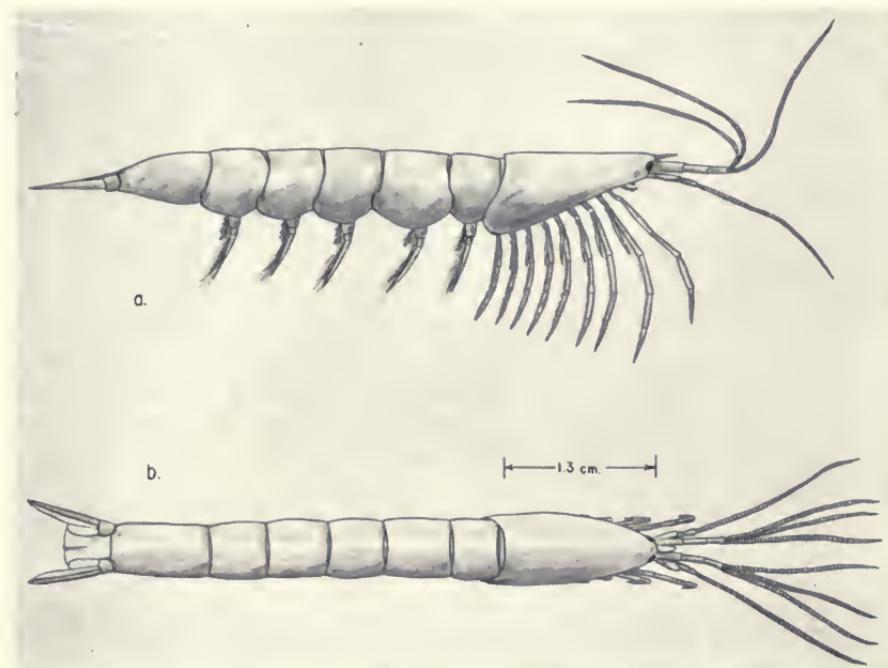


FIG. 111. Reconstruction of *Kallidecthes richardsoni*.

Family: **Kallidecthidae** new

No familial distinction is recognized at this time between the two known aeschronectidan genera. The characters of the family will remain for the time being as the characters of the order.

Kallidecthes new genus

Diagnosis.—Hoplocarid of moderate size; carapace free from at least the posterior thoracic segments; first antenna slightly shorter than the carapace, peduncle of three segments, three flagella; second antenna directed anteriad, laterad, and ventrad; eight thoracic legs, protopod with three segments, inner branch of four joints, outer branch as one, slim, elongate segment; second maxilla with four joints modified as a swimming appendage; first maxilla short; mandible with palp; rostrum short; abdomen long with enlarged second segment, last segment elongate and tapered; feathery gills associated with the pleopods; telson flattened and spade-like with no lobes or spines.

Genotype.—*Kallidecthes richardsoni* Schram, n. sp.

Remarks.—This very abundant crustacean in the Essex fauna represents a natant radiation of the hoplocarids. As such it forms

the basis of a new order, Aeschronectida. Several hundred specimens have been examined closely for this morphologic study. Occasionally immersion in xylene or glycerol was helpful in elucidating details.

Kallidecthes richardsoni new species. Figures 111-123.

Diagnosis.—Since but one species is known, the diagnosis of the species is that of the genus.

Description.—This animal was approximately 7 cm. long from the anterior point of the carapace to the posterior tip of the uropods. The carapace is subtriangular in outline. No doublure is present along the margins. The surface is smooth, having no furrows or processes. The carapace is deeply notched near the anterior apex to form a receptacle for the stalked compound eyes (PE9771, PE11227). The rostrum is relatively short and is movably articulated to the anterior of the carapace (PE9771, fig. 112).

The thoracic legs decrease in length from the anterior to posterior, the first thoracopod being about 2 cm. long and the eighth about 1 cm. The protopods are composed of three segments; the second, the coxa, is somewhat longer than the other two. The inner branch has four elongate segments. The outer branch is thin and blade-like, of one segment, and almost as long as the ischio-merus of the inner branch (PE8521, PE11409). The posterior edge of the inner branch is supplied with setae (H269). (PE8521 and PE11409, fig. 113; H269, fig. 114).

The second maxilla is very large and modified as a swimming appendage. The first three segments are short (PE11227, PE11242) the third joint being longer than the other two. These are apparently followed by four longer segments. There is no basis for drawing homologies between these segments and those of the thoracic legs. This second maxilla is shorter than the first thoracopod and is typically directed more anterior than downward. The process of the first maxilla is smaller than the second. The three-jointed palp can be seen projecting in front of the second maxilla (PE11227, PE11242). A tiny nubbin in front of the first maxilla (PE11227) is here interpreted as being the mandibular palp. No conclusions as to the details of this structure can be drawn (PE11242, fig. 115; PE11227, fig. 116).

The first antennal peduncle is composed of three segments, each succeeding one shorter than the preceding. The first antenna is tri-flagellate (HTP4245). The flagella are subequal in length and about

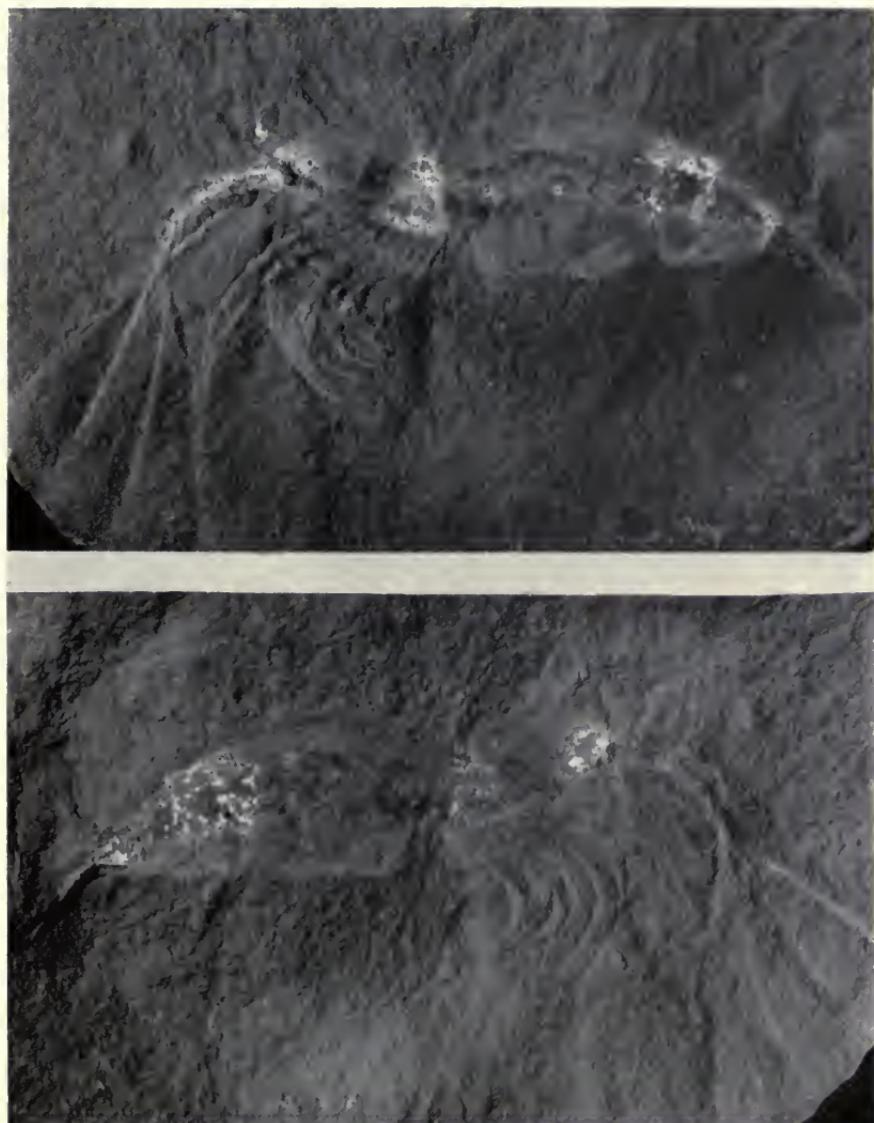
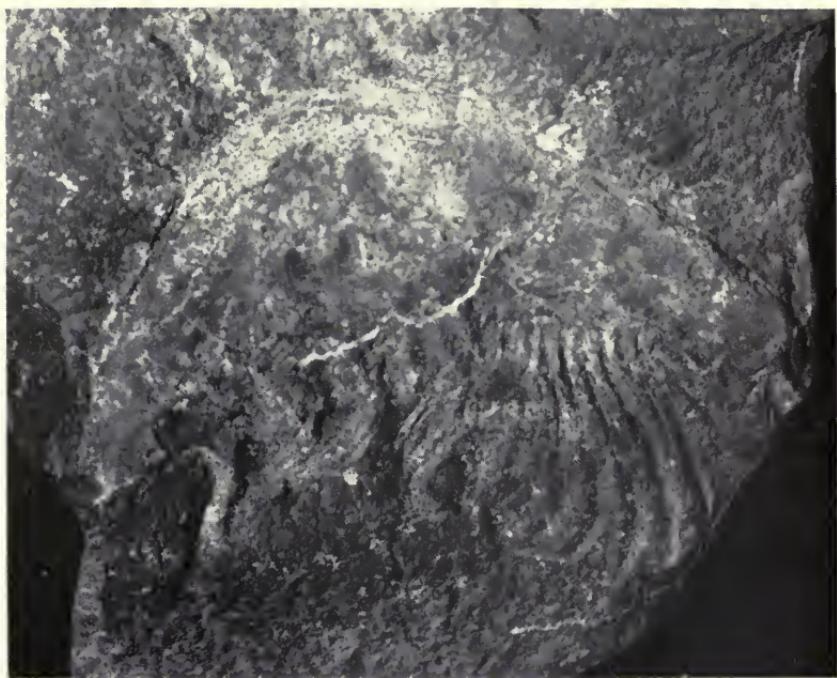


FIG. 112. *Kallidectes richardsoni*, PE9771, holotype. $\times 1.5$.

2 cm. long. The second antennal peduncle apparently has two segments (PE8508). Usually the demarcation cannot be clearly seen since the oval exopodal scale frequently covers most of the peduncle. The peduncle of the second antenna is about two-thirds the length of that of the first, and is typically directed downward.

The abdomen is about three times the length of the cephalothorax. The second pleomere is enlarged and its pleura overlap those



a



b

FIG. 113. *Kallidecthes richardsoni*, a. PE11409; b. PE8521, displaying appendages and the typical mode of preservation of this animal. $\times 2$.



FIG. 114. *Kallidecthes richardsoni*, H269, with setae on the thoracic legs. $\times 4.5$.

of the first as well as those of the third segment. This appears to be an adaptation to facilitate flexure. The fossils are frequently found doubled up with the principal bend occurring at this point. The sixth segment is elongate and tapered at its posterior end.

The pleopods are quite robust in the protopodal region. They are composed of a two-jointed protopod bearing flap-like endopods and exopods which have setae along their edges (PE12329). The gills are on the pleopodal coxa (H170 and PE12329, a gift of Mr. and Mrs. Francis Wolff) and appear to take origin on the anterior or medial surfaces. They are bifoliate. The longer branch is some 3 mm. in length. A shorter branch, about 1 mm., takes origin from very near the base of the gill. From these two primary arms secondary branches arise, and from these tertiary branchlets can be distinguished (PE12329 and H170, fig. 119).

Structural detail of the tail fan is very difficult to observe. The plane of the tail typically lies at right angles to that of the body plane (PE11221 and PE12265, a gift of Mr. Kenneth Davenport). The uropodal exopod is bordered laterally by a heavily chitinized margin and medially by a more membranous portion. The endopods are lobate and are about half the length of the exopods. The telson itself is paddle-like with a slight point on the midline of the posterior

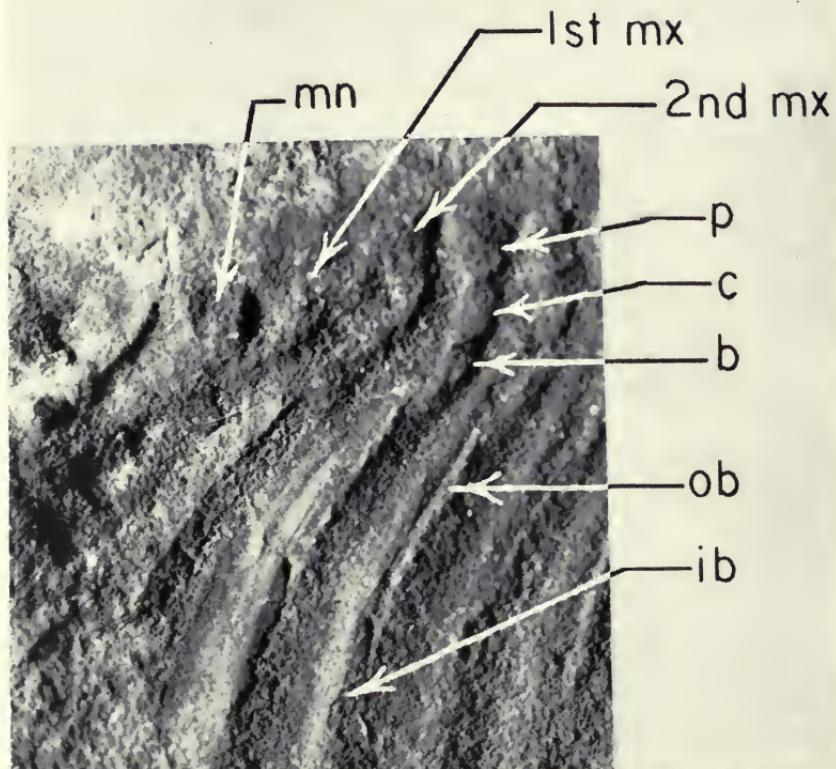


FIG. 115. *Kallidecthes richardsoni*, PE11242, (mn) mandible, (mx) maxilla. (p) precoxa, (c) coxa, (b) basis, (ob) outer branch, (ib) inner branch. $\times 1.5$ and $\times 5$.

margin. There are no indications of setae or spines along the margins of the uropods as there are in the other genus of this family, *Aratidecthes*. The entire tail fan appears well suited for swimming (PE12265, fig. 120).

Remarks.—The eight thoracic legs were all unmodified and employed as swimming appendages. Unlike the anterior thoracopods of the other hoplocarid orders, those of the aeschrongectids were not modified at their distal ends for food capture. It had also been implicitly assumed by most workers that the ancestral hoplocarid thoracopod probably corresponded to that expressed for the general caridoid by Calman (1909, p. 145). The thoracic legs of the aeschrongectids agree with this only in a general way. The protopod has three segments instead of two, there are four joints in the inner branch, and one undivided segment on the outer.

The use of the terms "inner" and "outer" branch is here employed since there is doubt as to which one is the true endopod or exopod. In the modern stomatopods the appendages on the posterior thoracomes also have a three-segmented protopod, a unisegmental outer branch (usually), and a bisegmental inner branch. Claus (1871) has demonstrated that the inner branch is really the exopod and the

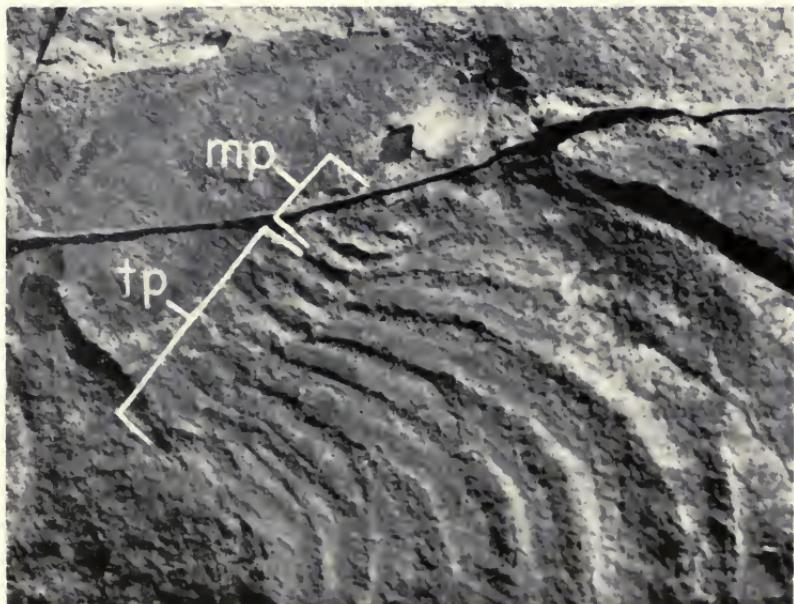


FIG. 116. *Kallidecthes richardsoni*, PE11227, with the mouth parts (mp) and thoracopods (tp) indicated. $\times 4.5$.

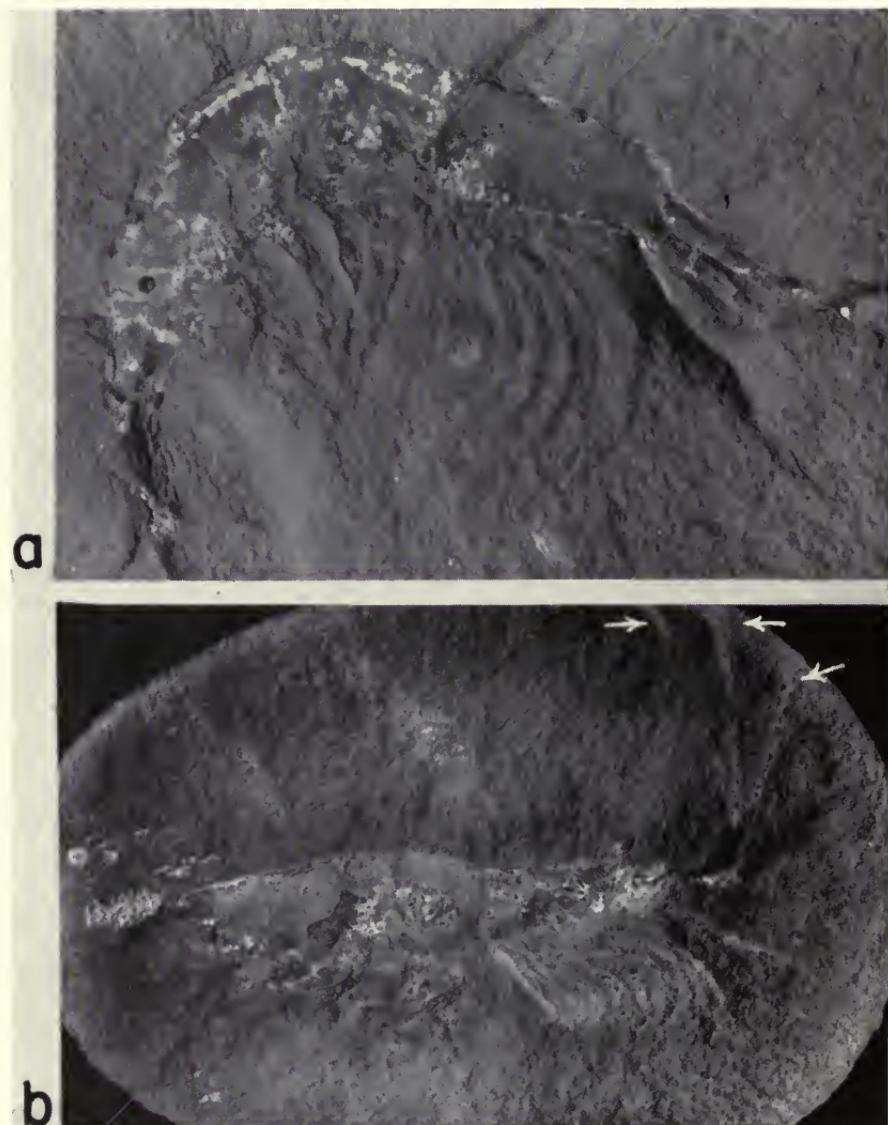


FIG. 117. *Kallidecthes richardsoni*, a. PE8508, showing the peduncular segments of the antennae; b. HTP4245, with triflagellate first antenna. $\times 1.5$.

outer branch is really the endopod; the positions become reversed during embryonic development. The possibility that this reversal might be true for the aeschronectids cannot be ruled out, especially since the general morphology of the posterior thoracopods of the stomatopod and the thoracic appendages of the aeschronectids agrees. Since embryologic evidence is not available, judgments can-

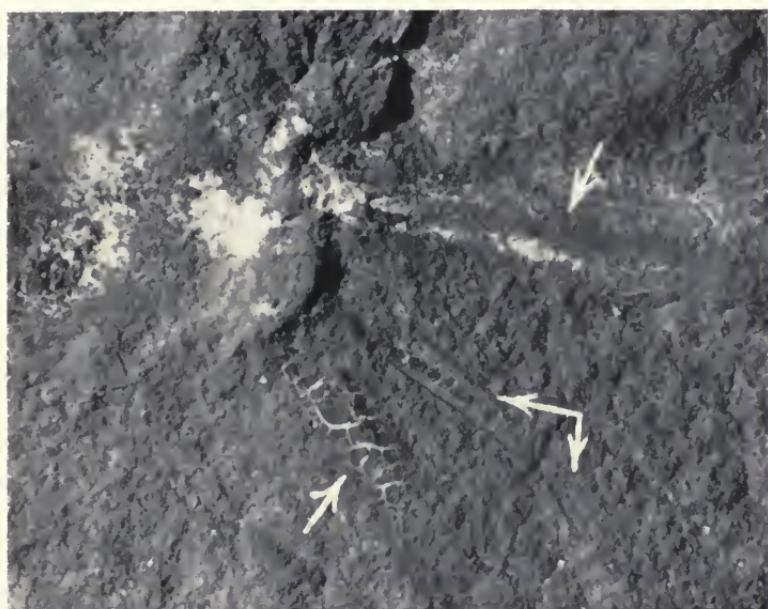
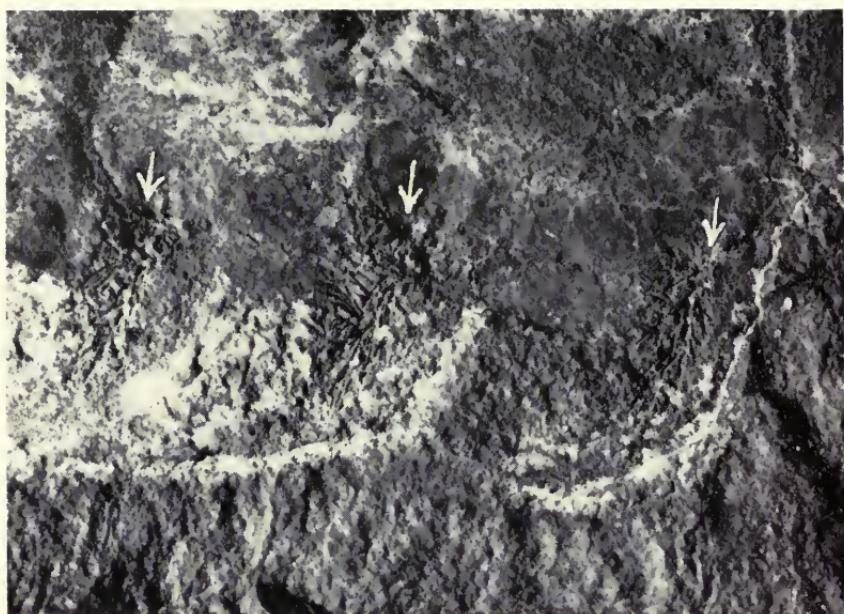


FIG. 118. *Kallidecthes richardsoni*, H162, with arrows indicating peduncle of first antenna, peduncle and flagellum of second antenna, and scale of the second antenna. Note the downward direction of the second antenna components. $\times 2.5$.

not be made. I, therefore, prefer to use the more generalized terminology of "outer" and "inner" branch.

Triflagelly is unique to the hoplocarid and palaemonid caridean first antennae. In both the stomatopods and the palaemonids the two outer flagella are associated at their bases. The stomatopods have all three about equally developed, though short. The palaemonids, however, typically have the accessory flagellum smaller than the associated one. This accessory flagellum varies from being well developed, as in *Pseudopalaemon*, rudimentary though still visible, as in *Paraclimenaeus*, to being practically absent, as in *Typton* (see fig. 121). The flagella of *Kallidecthes* are more akin to the stomatopod condition in that all three are equally developed.

One of the striking features of the stomatopods is the cephalic kinesis occurring at a point between the first and second antennae. It is not directly determinable whether the aeschronectids and palaestomatopods possess this kinesis since the carapace is so well developed that the critical area is covered, as in the Nebaliacea. Grobben (1919) made some observations on this region which might be useful in indirectly judging whether the aeschronectids have a cephalic



a



b

FIG. 119. *Kallidecthes richardsoni*, a. PE12329; b. H170, both displaying the feather-like gills on the pleopodal protopods. $\times 4$.



a



b



FIG. 120. *Kallidecthes richardsoni*, a. and c. right counterpart; b. left counterpart of PE12265, (pr) protopod, (en) endopod, (ex) exopod, (t) telson. $\times 2.3$.

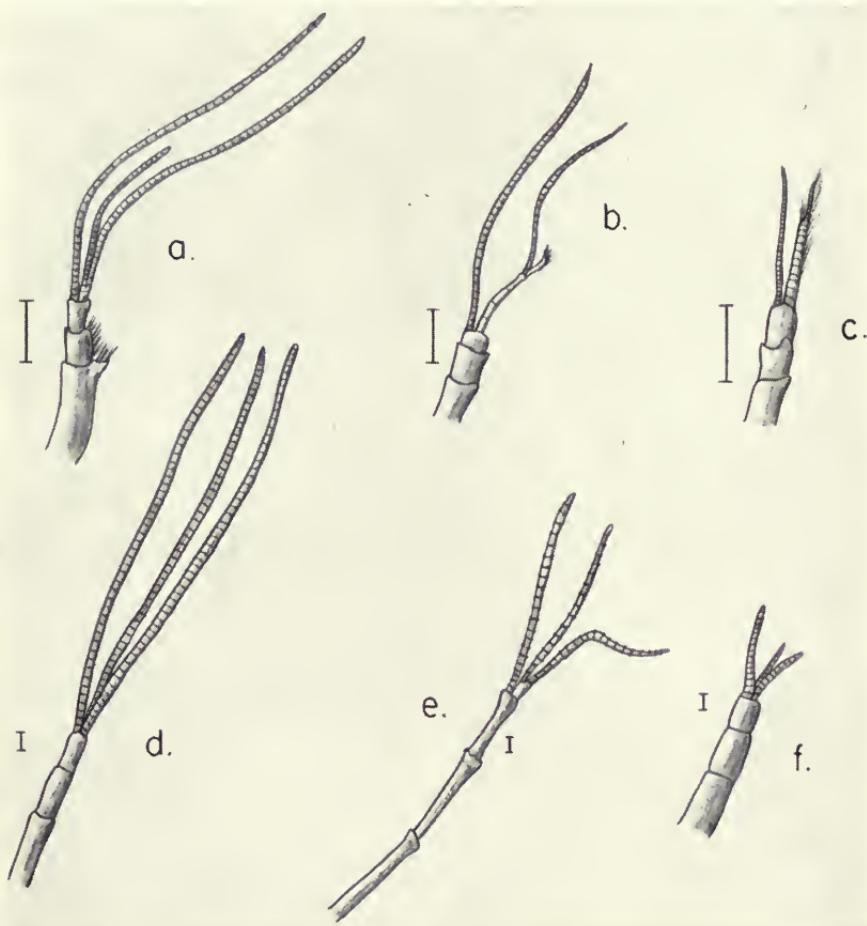


FIG. 121. Various types of triflagellate first antennae in palaemonids and hoplocarids; a. *Pseudopalaemon bouvieri*; b. *Paraclimeneus bermudensis*; c. *Typton spongicola*; d. *Kallidecthes richardsoni*; e. *Squilla mantis*; f. *Perimecturus elegans* adapted from Brooks (1969); scales indicate 1 mm. lengths.

kinesis. The second antennae in nebaliaeans and stomatopods are not directed entirely forward nor do they lie in the horizontal plane of the first antennae as they do in the modern caridoid malacostracans. Because there is a kinesis in the cephalon, the second antennae are required to direct themselves outward, downward, as well as forward (fig. 122). The second antennae of the aeschrongiectids conform to the pattern expressed in the nebaliaeans and stomatopods (fig. 118), rather than to the caridoids. This may be indirect evidence that the aeschrongiectids possessed a cephalic kinesis between the first and

second antennae. The reconstruction of *Perimecturus elegans* by Brooks (1969) might also warrant such a conclusion. Grobben further implies that the articulated nature of the rostrum is indirectly

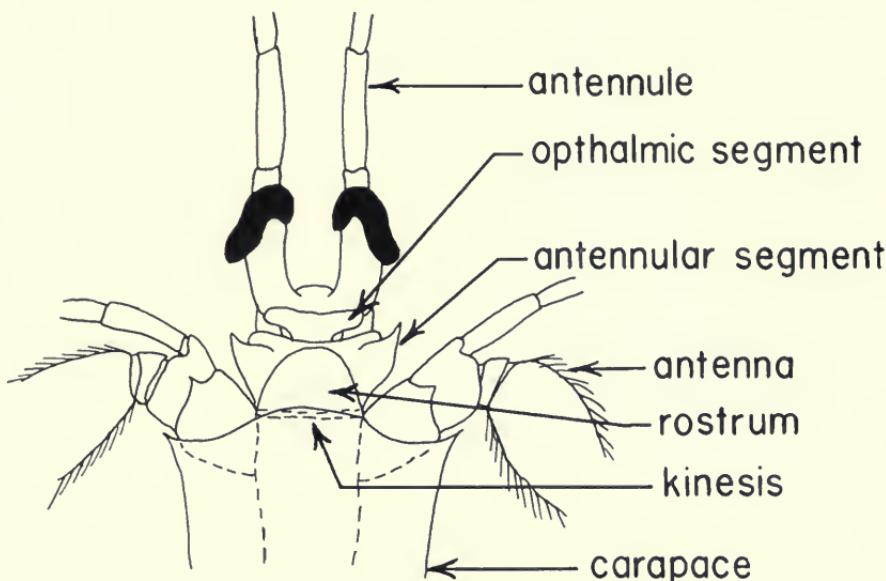


FIG. 122. Arrangement of structures around the cephalic kinesis of the stomatopods.

related to this kinesis, providing a movable portion of the carapace over the mobile cephalic area.

The preservation of the gills in these specimens is almost unprecedented in the fossil record. They differ from the gills of the stomatopods in that they are attached to the protopods (modified epipodites) and not to a "branchial appendage" near the base of the exopod. As far as can be determined, the aeschreunctid gills can be technically designated podobranchiate, dendrobranchiate types, i.e., originating on a segment with tertiary branchings in their fine structure. In general form they resemble somewhat the gills of euphausians.

Statistical data are presented in Table 1 based on 160 specimens in the collections of Mr. Jerry Herdina and Field Museum of Natural History. Statistical analysis is complicated by distortion of the fossils. *Kallidectes* is typically preserved on its side and undoubtedly underwent compression. There might be some difficulty in determining dead animals from exuviae. Specimens representing dead animals are characterized by detrital casts of the intestine and open or

TABLE 1.—Statistical data for various body measures (in centimeters) of *Kallidecthes richardsoni* based on measurements taken on 160 specimens. Because of small net sample size, the modes were not able to be determined for some of the parameters.

	N	average	s	md	mo	range
carapace length	144	1.26 ± .11	.16	1.29	1.28	1.56-.71
body length	68	4.26 ± .52	.59	4.36	4.44	5.73-2.35
antennule peduncle	34	1.08 ± .19	.18	1.08	—	1.65-.76
antennal peduncle	11	.78 ± .25	.13	.77	—	.95-.58
protopod and exopod of uropod	9	1.30 ± .46	.14	1.28	—	1.51-1.05

slightly flexed positions. Exuviae have a tendency to collapse and double up on themselves, or frequently the carapace and anterior appendages become detached from the abdomen and ventral posterior thoracic skeleton. Both exuvial states have been seen in some of the Essex fossils. Most specimens, however, appear to represent dead bodies. The exuvial preservational conditions were not used in collecting this data. Therefore, the data is taken to closely represent the original population.

Measures were made with a vernier caliper and recorded for specimens from which plausible measurements could be taken. No one specimen could be measured for all the characters under consideration.

The data for the carapace length is plotted in a histogram (fig. 123). The distribution is similar to what one would expect from a population of invertebrates. The distribution is skewed toward the larger sizes in the range. Clustering was observed around points at about 5 mm. intervals. This may reflect stages in growth and development.

Some inferences of the paleoecology of *Kallidecthes* can be made from the morphology. It appears that *K. richardsoni* was primarily a nektonic animal. The morphology of the setiferous appendages, especially the thoracopods, and the morphology of the tail fan are indicative of a swimming crustacean. It probably behaved not unlike the modern *Penaeus*, a moderate-sized decapod that swims about and intermittently comes to rest on the bottom.

The gut of *K. richardsoni* is frequently preserved as a detritus-filled cast. This might indicate a detrital or filter-feeding type of nutrition. Manton, however (Whittington and Rolfe, 1963, p. 160), has cautioned against a too hasty interpretation of such detrital fillings. The general morphology would seem to indicate a detrital or filter feeder, especially the setiferous thoracic legs (see fig. 114). One might also speculate that the shielding of the leg bases by the carapace might be correlated with a possible food channel on the under-

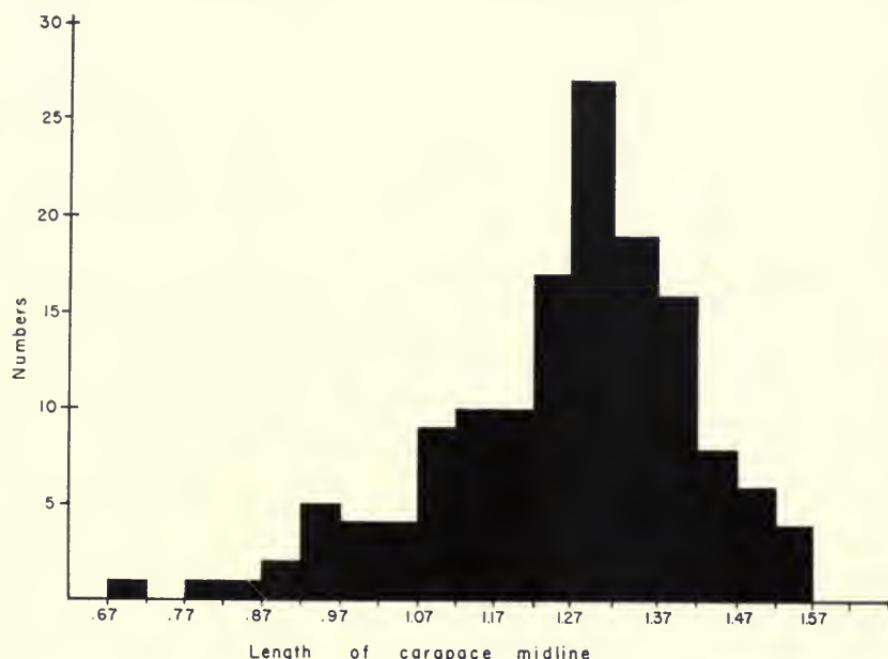


FIG. 123. Size frequency distribution of the midline length of the carapace of *Kallidecthes richardsoni* based on 144 specimens in the collections of Field Museum and Mr. Jerry Herdina. Length in centimeters.

side of the thorax. This arrangement would serve to help direct food forward to the mouth. The general morphology and appearance of *K. richardsoni* is not unlike modern detrital and filter feeders. It appears that *Kallidecthes* lived in a locality where a great deal of detrital or organic material occurred in the water; this habitat would serve to strengthen the above interpretation.

This crustacean is almost exclusively restricted to the Essex fauna. Only one specimen, USNM 161490, was found in a collection made in the Braidwood localities.

It is my great pleasure to name this unusual and important fossil malacostracan after my good friend and colleague, Eugene S. Richardson, Jr., of Field Museum of Natural History.

Holotype.—PE9771 (fig. 112).

Aratidecthes new genus

Diagnosis.—Hoplocarid of moderate size; carapace free from at least the posterior thoracic segments; first antenna large; eight thoracopods, unmodified in form, and undifferentiated from each other;

abdomen large with second, fifth, and sixth somites elongate; tufty gills on the pleopods; endopods of uropods brush-like with a thick lateral margin and the medial portion membranous and fringed with setae; telson spatulate.

Genotype.—*Aratidecthes johnsoni* Schram, n. sp.

Remarks.—Zangerl and Richardson (1963, pp. 125, 128, 135) mention the remains of a "percarid" found in Zones 5 and 6 of their Garryard Quarry profile. The black shale which they removed from the site in Parke County, Indiana, was an exposure of the humulite facies of the Logan Quarry shale of the Lower Wiley cyclothem, Middle Pennsylvanian. The original quarry site has since been destroyed. Though the animal represented is not part of the Mazon Creek faunas of slightly higher in the section, this crustacean has proved to be related to *Kallidecthes richardsoni*. I have, then, chosen to describe and discuss it here.

Much of the material is fragmentary. Preparation is difficult in this highly pyritic shale. Study was facilitated by using xylene. *In no case* should any water, water base, or hydrophilic materials be placed on this kind of shale because a chemical reaction immediately takes place forming a white powder of iron sulfate which obscures everything.

***Aratidecthes johnsoni* new species. Figures 124–128.**

Diagnosis.—Since but one species is known, the diagnosis of the species is that of the genus.

Description.—This crustacean was moderate in size, 7–8 cm. from the base of the flagellum to the tip of the uropods. The carapace is smooth, having no grooves or spines. There is a clear doublure along the posterior margin of the carapace (PE11870), but it is only faintly present along the ventral edge (PE11619). No definite rostrum has been preserved on any of the specimens at hand though a slight medial projection seems to be indicated (PE11870). The general outline of the carapace is trapezoidal (PE11619, fig. 125).

The antennae are poorly preserved. What has been exposed has appeared only after difficult preparation (PE11619, PE11870, and PE11871). The peduncles of the first antennae are very well developed and are apparently composed of three segments, though only the proximal one has been seen complete. These antennular peduncles are from 1.5 to 2 cm. long. The proximal portions of two closely associated antennular flagella can be discerned (PE11619). The charac-

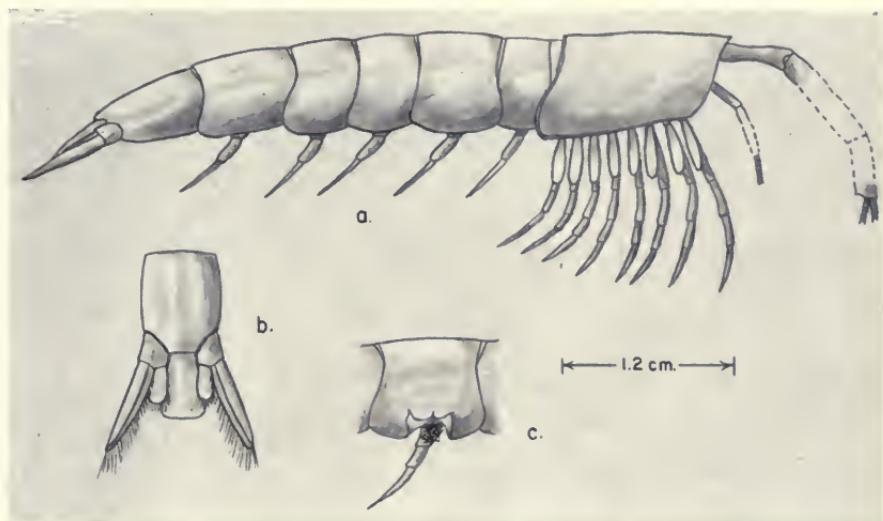


FIG. 124. a, Reconstruction of *Aratidecthes johnsoni*; b, dorsal view of tailfan; c, gills on second abdominal segment.

teristic third flagellum of the hoplocarids has not been seen. At least two segments compose the antennal peduncle, which, as a whole, is shorter than the antennular peduncle (PE11619, PE12178). Some organic material is present on PE11619 where the flagellum would have been (PE12178, fig. 126).

None of the eight thoracopods were modified as chelae or subchelae (PE12178). The protopods are located under the margins of the carapace. From the first few thoracopods on the left side it appears the protopod had three subequal segments. The outer branch is an oval flap almost as long as the ischio-merus. On the inner branch the ischio-merus is about .5 cm. long, the carpus shorter by half, the propodus shorter again by half, and the dactylus, tapering to a point, about the size of the carpus. The anterior edges of the three proximal joints of the inner branch as well as the margins of the flap of the outer branch are finely setous. There is no indication whatsoever that the second maxilla is modified like that of *Kallidecthes*.

The abdomen is about three to four times as long as the thorax. The first segment is small, the second enlarged with overlapping pleura to permit flexure. The third and fourth segments are again small, while both the fifth and sixth segments are elongate, the last being flattened toward the tail fan.

The gills are located on the lateral base of the abdominal legs just under the pleura of the pleomeres (PE11869). They are usually



FIG. 125. *Aratidecthes johnsoni*, PE11619, a. under xylene; b. under ordinary lighting. $\times 2$.

poorly preserved (PE11619, PE11868, PE11873, and PE12178). The pleopods themselves typically exist on these specimens as pyritic ghosts (PE11869, fig. 127).

The lateral margin of the uropodal exopods is blade-like (PE 11620). The inner margin is setiferous (PE11622 and PE11623). The endopods are simple flaps half the length of the exopods. The telson (PE12178) is spatulate, widening distally from the base (PE 11620, 11622, 11623, fig. 128).

Remarks.—The gills of *Aratidecthes* are tufty, while those of *Kallidecthes* are feathery. *Aratidecthes* gills are also thicker, with secondary and tertiary branchings, and are directed upward under the pleu-



FIG. 126. *Aratidecthes johnsoni*, PE12178, holotype. $\times 2$.



FIG. 127. *Aratidecthes johnsoni*, PE11869, arrows pointing to the bases of the plume-like gills. $\times 4.5$.

ron. These gills are consequently more protected than those of *Kallidecthes*, which may be related to *Aratidecthes'* mode of life and the habitat in which it lived.

The preservation of the material is such that measures given in Table 2 are only rough, especially those of overall abdominal length.

Zangerl and Richardson used the term "percarid" for the sake of convenience; this term was not meant to imply that this animal was a *peracarid*. The enlarged abdomen, shortened thorax with carapace, three-segmented thoracopodal protopods, and abdominal gills place *A. johnsoni* in relationship to the hoplocarids and *K. richardsoni*. The unmodified nature of the thoracic appendages indicates that it, like *Kallidecthes*, was probably capable of swimming.

Because of the nature of the material at hand no definite conclusions can be reached as to the degree of relationship between these two genera within the aeschronectids. Although the erection of a separate family for *Aratidecthes* might be warranted on the basis of the unmodified second maxilla, the flap-like nature of the outer branch, and the tufty nature of the gills, I have not felt justified in doing so at this time. The elongate form of the fifth and sixth pleomeres and the unmodified second maxilla may indicate a more primitive position for this genus than for *Kallidecthes*.

The fauna of zones 4 to 6 of the Garrard Quarry (*Myalina*; *Lingula*; some snails; small paleoniscoids; a rhipidistian identified by some bones, scales, and teeth; a freshwater pleuracanthid shark; and an acanthodian) prompted Zangerl and Richardson to identify these levels as representing a freshwater environment. These zones are succeeded by marine burial communities containing mostly *Dunbarrella* and cephalopods. Zones 5 and 6 contain great quantities of sulfides, which suggested to the authors that the bottom conditions in these zones, at least that below the topmost layers, were very poisonous. Because there was no evidence of mass mortality or of bottom disturbance, they further concluded that the overlying water was not toxic and permitted normal activity.

The size of the antennules of *Aratidecthes* is typical of those found among modern reptant forms. Though the thoracic legs are slender, they are well developed and were probably capable of supporting the animal on the bottom. It would appear that *A. johnsoni* was nektonic, living on the bottom with sorties into the medium above. But since the bottom, or at least that below the immediate surface zone, appears to have been toxic in this locality, it is possible that the indi-

TABLE 2.—Measurements of *Aratideches johnsoni* given in centimeters.

Specimen	Carapace length	Carapace depth	Abdominal length	Length of individual abdominal segments					
				1	2	3	4	5	6
PE11616			.4	.7	.6	.5			
PE11617			3.2		.3	.4	.7		.8
PE11619	1.2	.9	>3.2	.4	.5	.4			
PE11870	1.3	.9	3.4						
PE11871			3.8	.4	.7	.6	.5		
PE11872						.4	.5	.6	.7
PE12178*	1.1	.8		.5	.5	.4	.5		.6

* Holotype.



a



b



c



d



e

FIG. 128. *Aratidecthes johnsoni*, a. PE11616, with thorax, anterior abdomen, and parts of pereiopods; b. PE11617, abdomen and part of tail; c. PE11623, tail; d. PE11622, tail; e. PE11620, tail. $\times 2$.

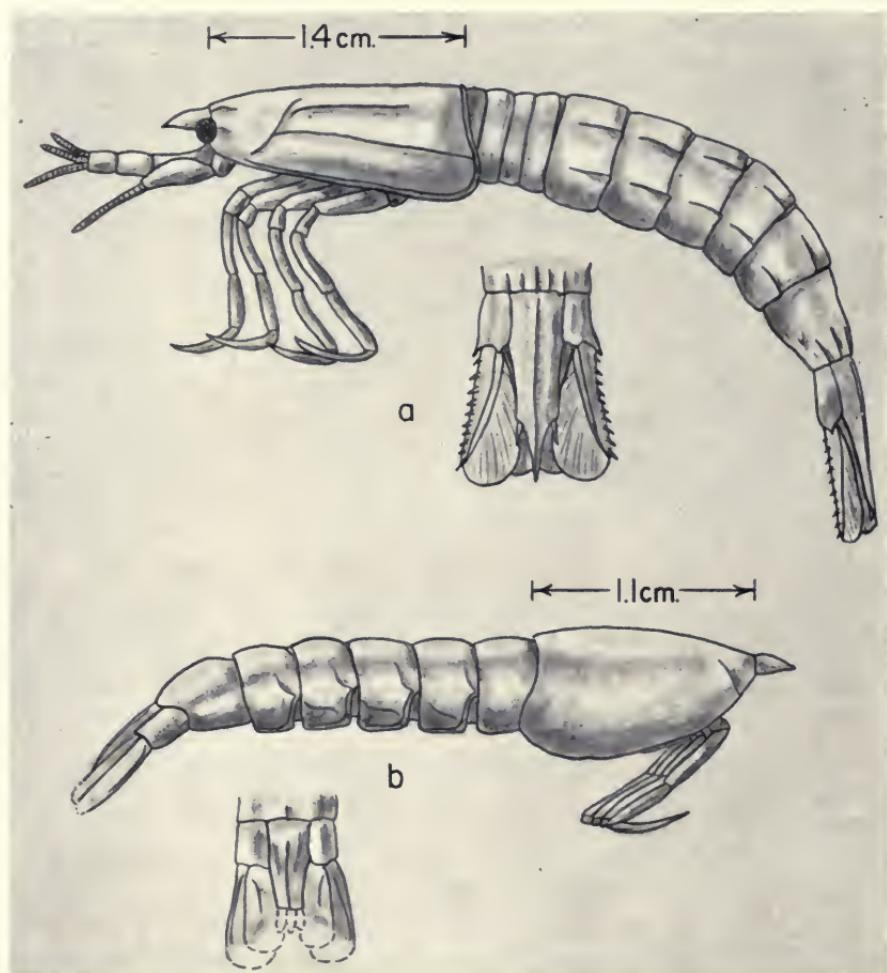


FIG. 129. Reconstructions of, a, *Perimecturus elegans* and, b, *Archaeocaris vermiciformis*, 1969 adapted from Brooks (1962).

viduals represented are those that wandered into this pool and succumbed. The cleanly broken and fragmentary nature of much of the material may represent residues of fish meals.

This animal is named in honor of Ralph Gordon Johnson, my friend and advisor, of the University of Chicago.

Holotype.—PE12178 (fig. 126).

Order: Palaeostomatopoda Brooks, 1962

Carapace covering thorax or reduced, lateral wings developed; thorax not sharply regionalized; thoracic segments shorter than the

abdominal segments; thoracopods 2-5 developed as subchelae with the ischio-merus short and the carpus long; telson with caudal lobes.
Miss.-Penn.

Family: **Perimecturidae** Peach, 1908

The characteristics of the family are those of the order. Brooks (1962 and 1969) has recognized two genera, *Perimecturus* Peach, 1908, and *Archaeocaris* Meek, 1872.

Order: **Stomatopoda** Latreille, 1817

Carapace partially covering the thorax; the thorax sharply regionalized, the posterior three segments are about as large as those of the abdomen, the anterior segments are much reduced; at least thoracopods 2-5 with subchelae, the ischio-merus and carpus both primitively shortened; the telson without caudal lobes in the sense of Brooks (1962). *M.Penn.-Rec.*

Suborder: **Archaeostomatopodea** new

Carapace with lateral wings well developed; thoracopods 2-5 subequal in size with subchelae; the second through fifth thoracomeres are all separate and linearly arranged, not partially fused; telson subtriangular; uropodal exopod unisegmental. *M.Penn.*

Family: **Tyrannophontidae** new

Characters of the family are the same as those of the suborder.

Tyrannophontes new genus

Diagnosis.—Small- to medium-size hoplocarid; carapace free from the thorax, extending along its mid-dorsal line to the fifth somite and along its lateral margin to about the seventh; rostrum triangular; eyes stalked and ovoid; antennal peduncles short, the exopod of the second antenna developed as a very large lappet; anterior thoracic segments shorter than the posterior three, which in turn are only slightly shorter than those of the abdomen; the uropods have a uni-segmental protopod and blade-like exo- and endopods; telson triangular.

Genotype.—*Tyrannophontes theridion* Schram, n. sp.

Remarks.—This Essex crustacean is quite rare. It effectively extends the range of the stomatopods from the Jurassic back to the Middle Pennsylvanian. It forms a link between the palaeostomatopods and the later stomatopods yet it is sufficiently different from the latter to justify the erection of suborders within the Stomatopoda.

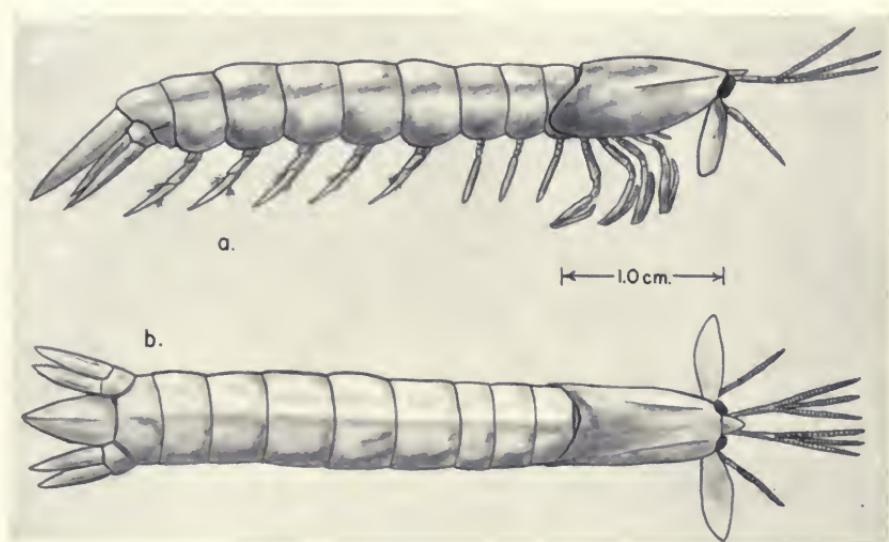


FIG. 130. Reconstruction of *Tyrannophontes theridion*; a, lateral view; b, dorsal view.

***Tyrannophontes theridion* new species. Figures 130–136.**

Diagnosis.—Since only one species is known, the diagnosis of the species must be the same as that of the genus.

Description.—The carapace is subrectangular in dorsal view and triangular in side view. The lateral wings are well developed so that the thorax is enveloped on three sides. The postero-lateral corners extend back beyond the mid-dorsal margin to the level of the seventh segment. There appears to be a slight gastric ridge extending from either side of the rostral base toward the postero-lateral corners (H182 and PE11403). The rostrum appears to be triangular (H182, fig. 131; PE11403, fig. 136).

The last three thoracic segments are not covered dorsally by the carapace. They are also larger than the segments which precede them and that carry the subchelate thoracopods. This regionalization is more pronounced than that of the palaeostomatopods but not as extreme as that of the stomatopods. Not only are the anterior thoracic segments reduced in size in the modern stomatopods but some degree of fusion takes place. The carapace of *T. theridion* is not fused to the anterior thoracomeres. The entire length of the thorax is slightly less than that of the abdomen.

The first antenna has three subequal flagella on it (W88). The peduncle is relatively short. There are indications of at least two, possibly three, peduncular segments of the antennule (H54). The



a



b

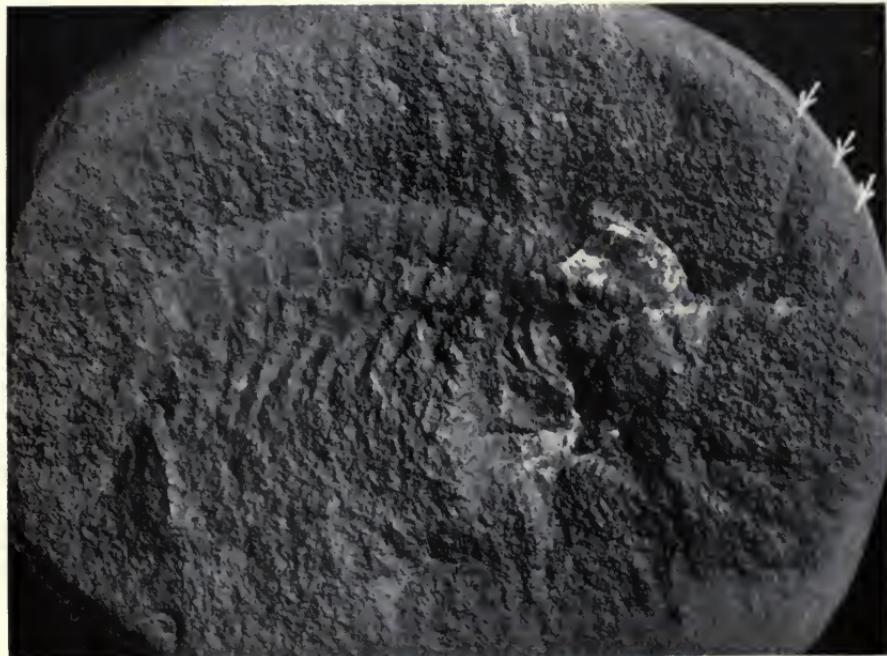


FIG. 132. *Tyrannophontes theridion*, W88, with triflagellate first antenna. $\times 1.5$.

second antenna, directed laterad and ventrad, has a relatively short flagellum and apparently two peduncular segments. The scaphocerite is very large and oval (H182). The compound eyes are stalked and oval in shape (H195, H54, and H172). (H172, fig. 131; W88, fig. 132; H54 and H195, fig. 133).

Thoracopods 2-5 are modified as subchelae (H172 and PE12098). The preoxa and coxa are short while the basis is as long as both of these together. The ischio-merus and carpus are short, as are those of the modern "mantis shrimps." The propodus and dactylus are long, forming the subchelae. No indications of teeth have been seen on the subchelar components. (H172, fig. 134; PE12098, fig. 135).

PE12098 displays some structure for the first thoracopod and the second maxilla. The details are obscure, however. The first thoracic leg appears to have at least four segments, the most distal one being the longest. Two segments can be detected on the second maxilla. The structure of the posterior thoracic legs is also obscure; a three-

FIG. 131. *Tyrannophontes theridion*, a. H172; b. H182, effectively displaying the antennal scale, unadorned exposed somites, and triangular telson. a, $\times 1.5$ and b, $\times 2$.

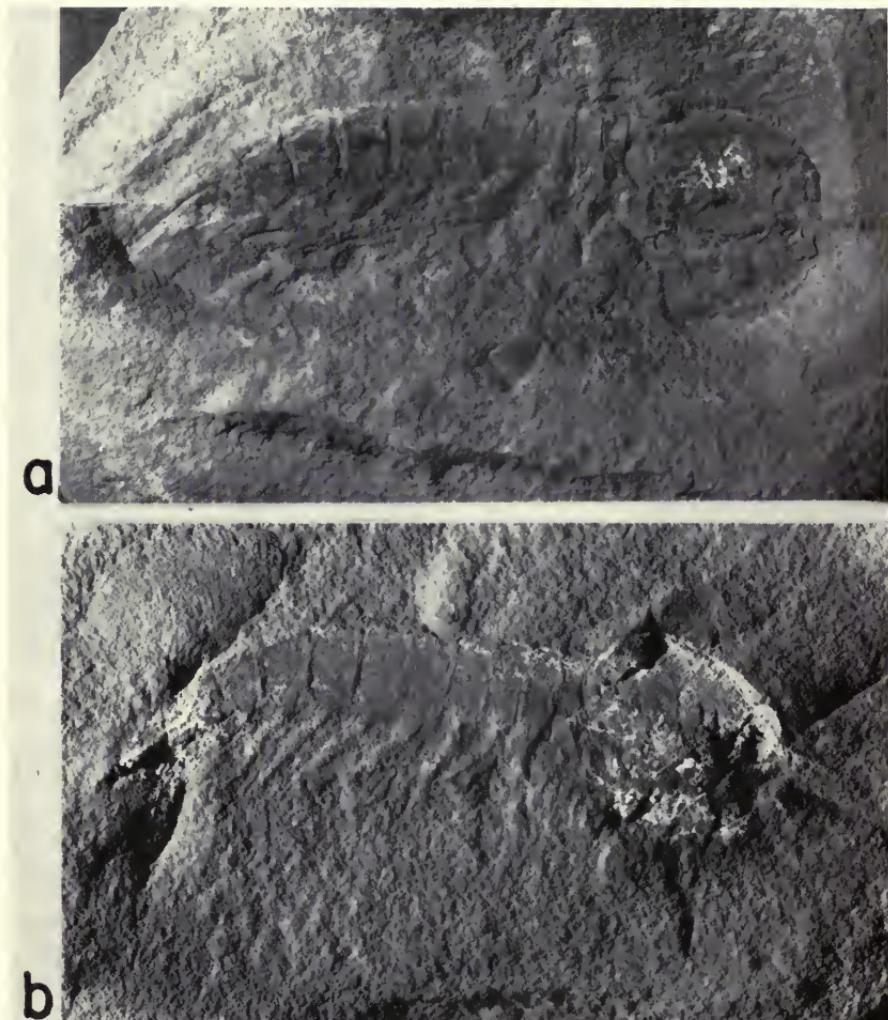


FIG. 133. *Tyrannophontes theridion*. a. H195, showing the carapace outline and the smooth tergites of the exposed segments; b. H54, with posterior thoracic and abdominal appendages. $\times 1.3$.

jointed protopod is followed by a single-jointed outer branch (PE 12098).

The pleomeres are all subequal. There is no tergal decoration on these or any of the exposed segments of the thorax. The pleopods have a two-jointed protopod and unisegmental rami. There is a suggestion of gills associated with the rami (H172). The telson is triangular in outline with a very slight median carina. The uropods

have unisegmental protopods with blade-like unisegmental exopods and endopods. There is no trace of a posterior process on the protopod (H172, fig. 136).

Remarks.—*Tyrannophontes* appears to form a morphologic intermediate between the palaeostomatopods and the later stomatopods. The carapace is reduced posteriorly, as in the stomatopods, but the lateral wings covering the side of the thorax and the anterior shield protecting the anterior cephalon are well developed, as in the palaeostomatopods. The thoracic segments are regionalized into an anterior tagma of reduced, thoracopod-carrying segments and a posterior tagma of "abdominalized" somites. This is more reminiscent of the stomatopods. On the other hand, all the anterior thoracopods bearing subchelae are of approximately equal size, and the thoracomeres have not undergone fusion. The ischio-merus and carpus of *T. theridion* are both short. In the stomatopods the thoracopods of somites 3, 4, and 5 have short ischio-meri and carpi. In the large specialized thoracopod of the second thoracomere the ischio-merus is modified

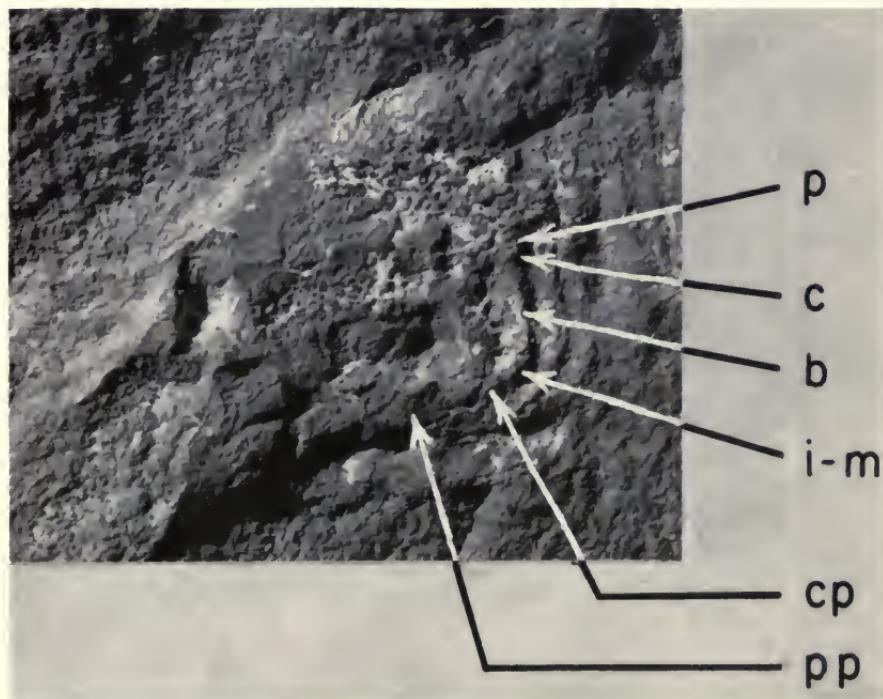


FIG. 134. *Tyrannophontes theridion*, counterpart of H172, (p) preoxa, (c) coxa, (b) basis, (i-m) ischio-merus, (cp) carpus, (pp) propodus. $\times 3$.

and enlarged. In the palaeostomatopods the carpus is elongate and the ischio-merus is reduced.

It would appear from the morphology that *Tyrannophontes* functioned much like the modern stomatopods. The subchelae were certainly employed in tearing apart captured prey. No judgments can be offered as to whether the tyrannophontids burrowed as do the recent stomatopods. Their rarity among the Essex crustacea is probably due to competition from the other carnivores and scavengers found among the Crustacea of this locality. In particular, *Belotelson magister* Packard, 1886 or some of the pygocephalomorphs, would have provided competition for *Tyrannophontes*.

It is also interesting to note that the typical position of preservation of these animals is on their sides. The later fossil stomatopods are always preserved on their dorsal or ventral surfaces. It appears that the body of *T. theridion*, while perhaps not laterally compressed, was at least cylindrical in cross-section. It is quite likely that with their somewhat fusiform shape, the tyrannophontids were capable of swimming activity.

Holotype.—PE12098 collected by Calvin George of Naperville, Illinois, and generously donated to the collections of Field Museum (fig. 135).

With the subordinal distinction of the Tyrannophontidae it becomes necessary to erect a suborder for the other families of Stomatopods.

Suborder: *Opisterostomatopodea* new

Lateral wings of the carapace poorly developed or absent; thoracopods 1–5 subchelate and of different sizes, the first being very small, the second very large and robust, the rest medium in size and subequal; the anterior thoracic segments reduced and partially fused into each other; telson broad, subrectangular in outline; uropodal protopods typically with a marked posterior process. *Jur.-Rec.*

Family: *Sculdidae* Dames, 1886

Uropodal exopod with one segment which has a series of movable spines on the outer margin. *Jur.-Cret.*

Family: *Squillidae* Latrielle, 1803

Uropodal exopods of two segments; sharp median carina on telson; telson with more than four intermediate denticles on the margin. *Cret.-Rec.*

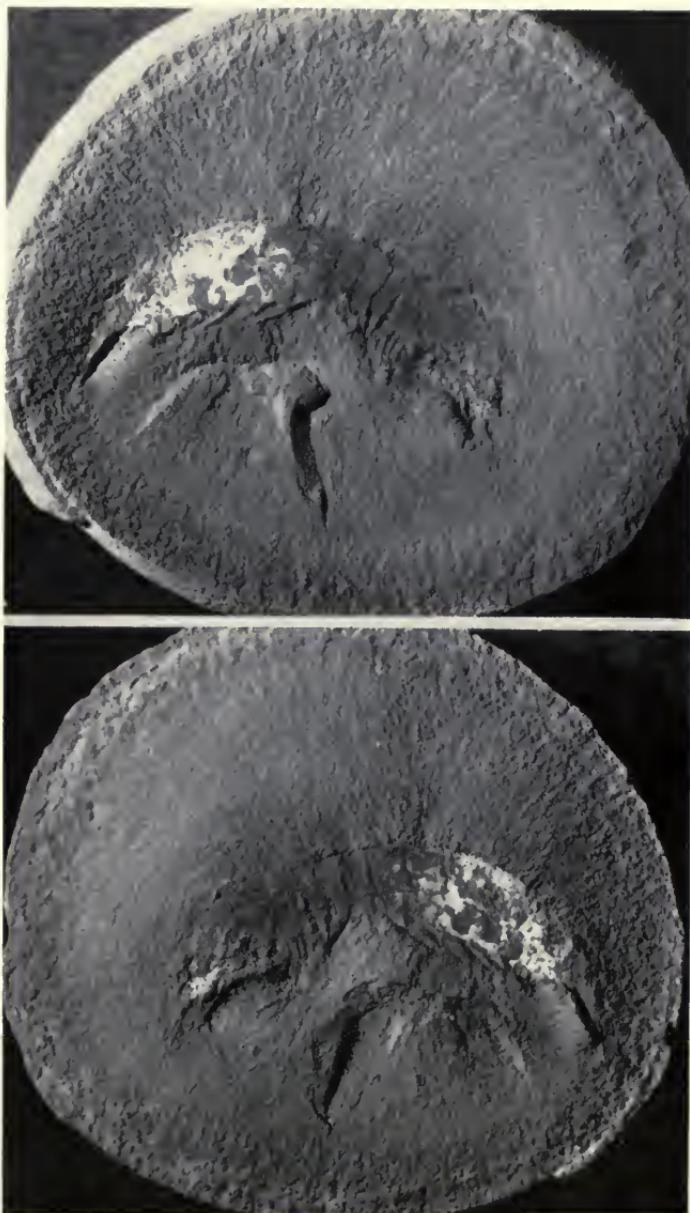
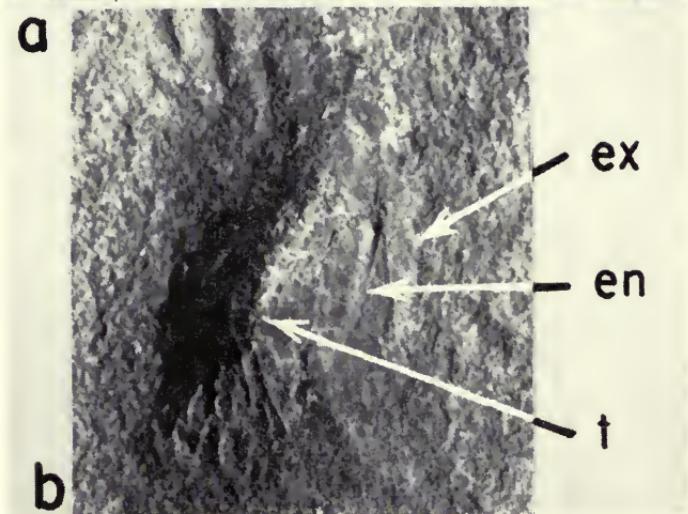


FIG. 135. *Tyrannophontes theridion*, PE12098, holotype. $\times 1.4$.



a



b

FIG. 136. *Tyrannophontes theridion*, a. H172, with arrows indicating gill-like structures on the rami; b. PE11403 (a gift of Mr. and Mrs. Ted Piecko), tail fan, (ex) expod, (en) endopod, (t) telson. $\times 2.2$.

Family: Gonodactylidae Giesbrecht, 1910

Uropodal exopods of two segments; median carina on telson; telson with fewer than three intermediate denticles on the margin. *Cret.-Rec.*

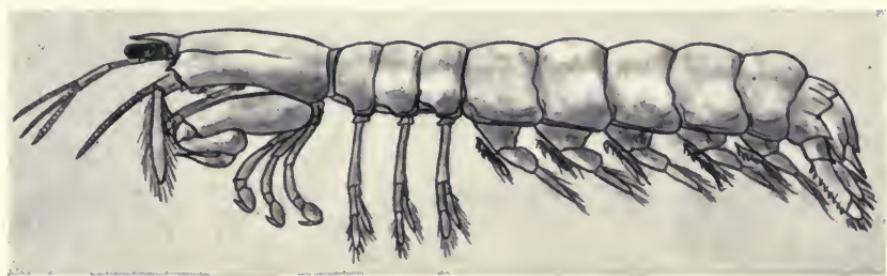


FIG. 137. A modern stomatopod of the genus *Gonodactylus*.

Family: Lysiosquillidae Giesbrecht, 1910

Uropodal exopods of two segments; no median carina on the telson. *Rec.*

Family: Bathysquillidae Manning, 1967

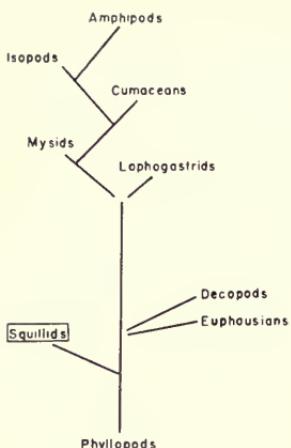
Uropodal exopods of two segments; telson with median carina; marginal denticles of telson with movable apices. *Rec.*

PHYLOGENETIC CONSIDERATIONS

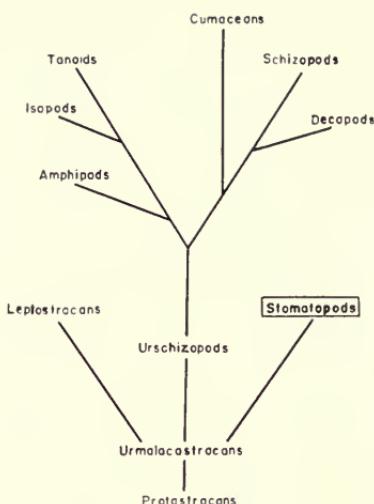
The hoplocarids, or more specifically, the stomatopods, have been the subject of divergent phylogenetic interpretation through the years (fig. 138).

Huxley (1867) proposed that if the nature of the eyes is ignored the stomatopods are most like the edriophthalmids (especially the amphipods) rather than the podophthalmids. He pointed out that the five anterior thoracopods are directed forward as they are in the amphipods. He also observed that the free segments of the thorax and abdomen are quite large in comparison to the carapace. The proportion between the head shield and the rest of the body in the stomatopods is most like that of the edriophthalmids.

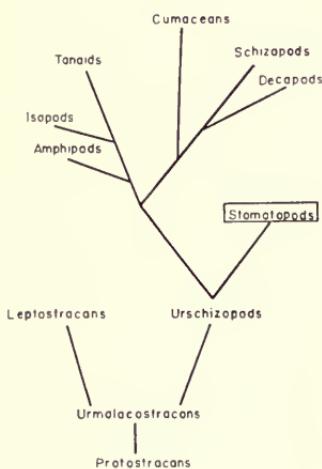
Boas (1883) was impressed by the characters the stomatopods shared with the euphausians and decapods. The mandibular structure, morphology of the maxilla, the appendix interna on the pleopods, and the presence of a petasma on the males all suggested affinity with the latter two groups. He believed the structure and location



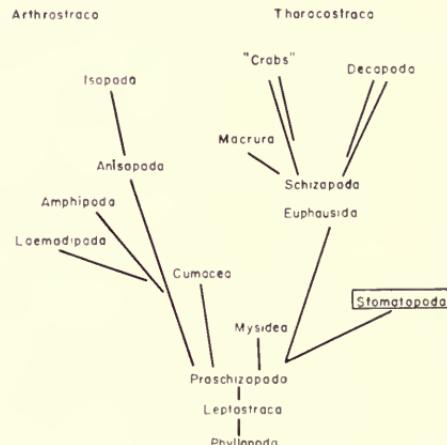
BOAS (1883)



CLAUS (1885)

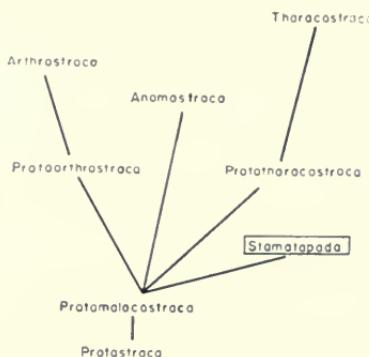


GROBBEN (1892)

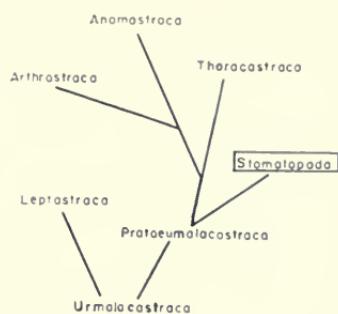


HAECKEL (1896)

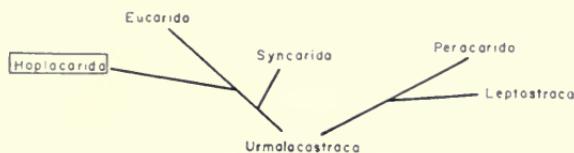
FIG. 138. Phylogenetic interpretations of the Malacostraca taken from the indicated authors. The hoplocarids set off with boxes.



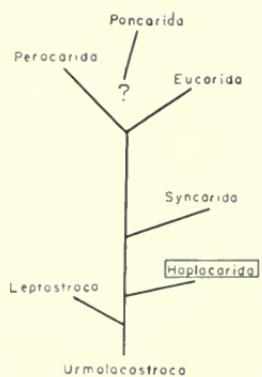
GIESBRECHT (1913)



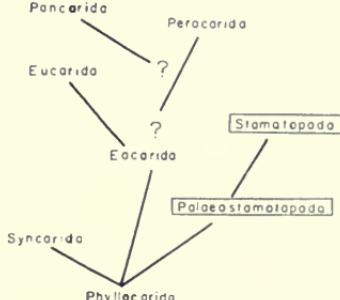
GROBBEN (1919)



GIESBRECHT & BALSS (1932)
BALSS (1938)



SIEWING (1956)



BROOKS (1962)

FIG. 138. *Continued*

of the heart, presence of maxillary glands in the larvae, and development of the uropods after the anterior pleopods were primitive characters. He placed the squillids on his phylogenetic tree near the euphausians and decapods, just above the "phylopods."

Claus (1885) advocated an even more divergent position for the stomatopods. He conceived of three lines developing from the *Urmalacostraca*: leptostracans, *Urschizopoden*, and stomatopods. He believed the multi-chambered heart and the carapace fused to the anterior thoracomeres to be primitive. He viewed as specializations the form of the thoracopods, the structure of the gut, and the location of the heart. He also regarded some embryologic patterns as primitive, such as the manner of the development of the hepatic diverticula.

Grobben (1892) agreed with Claus' general scheme of relationships but believed the stomatopods arose from the *Urschizopoden*. The schizopodous nature of the thoracic legs of the Antizoea larva indicated to Grobben a higher level of origin.

Haeckel (1896) essentially adopted Grobben's position. He placed the stomatopods in his order Thoracostraca as the earliest offshoot of the *proschizopods*.

Calman (1904, 1909), in establishing the modern system of classification for the Malacostraca, remained uncommitted to any definite phylogenetic scheme. He considered it most likely that the hoplocarids were an offshoot of the main stem of the Malacostraca.

Giesbrecht (1913) considered the heart with segmentally arranged ostia as primitive. Because of the abdominal gills, long digestive caeca, and five specialized "maxillepeds," he isolated the stomatopods from the rest of the thoracostracans. His phylogenetic scheme agrees with that of Haeckel in broad outline except that the basic eumalacostracan groups arise from a *protomalacostracan* rather than an ancestral schizopod. In this regard it is more akin to the "cari-doid theory" advanced by Calman (1909).

Grobben (1919) took up the question of stomatopod relationships again when he examined the anterior head anatomy of *Squilla* in relation to that of other Malacostraca. Instead of an *Urschizopod* ancestry for the Eumalacostraca, a *protoeumalacostracan* was envisioned as the prototype. In this regard he was influenced by Haeckel and Giesbrecht. Grobben was the first to emphasize the characters which associate the stomatopods with the leptostracans. The movably articulated rostrum and the muscle anatomy of the cephalic kinesis

TABLE 3.—Measurements of *Tyramphonites theridion* given in centimeters.

Specimen	Carapace length	Thorax length	Abdomen length	Thoracic segments			Individual abdominal segments					Telson
				3-5	6-8		1	2	3	4	5	
PE12098*	1.18	1.13		.38	.19		.20	.21	.19	.19	.15	
PE11403	.62	1.14		.50								
H54	.97	2.08	2.31	.35	.60	.32	.35	.36	.37	.39	.35	1.03
H142	.60	1.07	1.30									.47
H172	.74	1.63	1.57	.23	.56	.25	.28	.30	.28	.26	.37	.55
H182	1.13	1.83	1.89	.38	.74	.33	.36	.38	.38			1.0
H195	1.50	3.20	2.85	.63	1.11	.50	.54	.55	.52	.50	.41	.97
H261	.67	1.36	1.70		.52	.28	.30	.26	.25	.25	.23	.56
H262		1.32				.25	.26	.26				.57

* Holotype.

were adduced as most closely resembling these structures in the leptostracans. The second antennae in the leptostracans and stomatopods, placed behind the kinetic joint, are directed laterad, ventrad, and anteriad while in the higher malacostracans they are directed forward and displaced more toward the apex of the cephalon. The form of the sperm in the stomatopods is also similar to that of the nebaliaeans. Grobben viewed as specialized the dorso-ventral flattening of the body, the reduction of the carapace, the subchelatization of the anterior thoracopods, the enlargement of the abdomen, and the location of gills on the pleopods. He thus conceived of the eumalacostracan tree as being two-branched, one consisting of the hoplocarids and the other of the rest of the Eumalacostraca.

Komai (1924), in examining the early embryonic, pre-larval stages of *Squilla oratoria*, concluded that the closest agreement was with the nebaliaeans, rather than with the decapods or schizopods.

Giesbrecht and Balss (1933) and Balss (1938) viewed the Malacostraca as two divergent lines with the eucarids, hoplocarids, and syncarids on one hand, and the leptostracans and peracarids on the other. The carapace with its cervical groove was interpreted as allying the hoplocarids with the eucarids and syncarids. In some ways the hoplocarid appendages resemble those of the eucarids, *viz.*, in the numbers of segments in the antennal peduncles, resemblance of mouth parts, the pleopodal appendix interna, and the general form of the uropods. These similarities, however, are not at all striking and can be easily explained by convergence due to similarity of habit. The abdominal gills and elongate heart were interpreted as secondary. The nervous system, especially the brain and X-organ, was considered to be decapod and mysid in character. Several other features of internal anatomy were considered by these workers but their anatomical nature is too varied throughout all the Malacostraca to be of much use as phylogenetic indicators.

Komai and Tung (1931), in their study of the circulatory system of *Squilla oratoria*, discovered a peculiar condition of the stomatopod anatomy. The first abdominal segment is supplied by two sets of arteries. The arteries of the first abdominal segment end blindly in a muscle mass in the anterior portion of the somite. The appendages and remaining tissues of the first abdominal segment are supplied by an arterial network which actually leaves the heart in the anterior portion of the second abdominal segment; the appendages and tissues of the second abdominal segment are supplied by arteries from the third segment; those of the third by arteries from the fourth; those

of the fourth by arteries from the anterior fifth; those of the fifth by arteries which leave the heart in the posterior region of the fifth segment; those of the sixth by arteries from the sixth. Stomatopods, like all other Eumalacostraca, descended from leptostracans, which have seven abdominal segments. Siewing (1956, and in Whittington and Rolfe, 1963, p. 93) concluded from this evidence that, unlike the other Eumalacostraca, the stomatopods lost the first segment of this primitive series of seven instead of the sixth, as is apparently the case in the other Eumalacostraca. In other words, what is now the first pleomere was actually the primitive second pleomere, what is now the second was the primitive third, and so on.

On the matter of the seventh abdominal segment of stomatopods, Shiino (1942) has observed the development of a distinct extra set of ganglia and mesodermal thickenings in the sixth segment of *Squilla oratoria* during embryogenesis. These structures later fuse with those of the sixth segment as they do in *Hemimysis* (Manton, 1928). Shiino's observations would apparently contradict Siewing's interpretation above.

Siewing (1956) has set forth the most complete analysis of malacostracean relationships to date. He rejected the contention that the stomatopod heart and abdominal gills are secondary. The seven pairs of ostia and the seven pairs of lateral arteries indicate the primitive nature of the heart. The agreement in structural detail between the cephalic kinesis of the stomatopods and leptostracans is too striking to be considered convergent. He believed the extension of the heart and gonads throughout the body, the presence of a carapace, the segmental squama on the antenna, a naupliar eye, segmental uropodal exopod, and paired and unpaired frontal organs to be primitive. He viewed the subneural artery, loss of the primitive first pleomere, subchelate thoracopods, simplification of the last three thoracomeres, and the adult form of the carapace to be specialized, indicating a long history for the stomatopods. He placed them as an early offshoot of the main malacostracean stem.

Glaesner (1957) returned to a Haeckelian position by deriving all the Eumalacostraca with carapaces from the pygocephalomorphs and those without a carapace from the syncarids.

Brooks (1962) tentatively placed the primitive palaeostomatopods in the extinct superorder Eocarida. He indicated that they were probably ancestors of the stomatopods. He later (1969) re-located them into the Hoplocarida. The evidence indicated to him



a

b



FIG. 139. a. Abdominal "gills" of *Callianidea laevicauda*; b. abdominal gills of *Gonodactylus*. $\times 2.2$.

(Whittington and Rolfe, 1963, p. 162) that the stomatopods were not a separate line but joined the other Eumalacostraca at the phyllocarid level.

Secretan (1967) allies the stomatopods with her primitive pygaspids. Although Secretan does not recognize them as such, her pygaspids are in fact pygocephalomorphs, specifically of the family Notocarididae (see Schram, 1969).

Holthuis and Manning (1969) adopt the scheme presented by Siewing.

The definition of a hoplocarid varied from author to author, depending on the phylogenetic interpretation he adopted. The definition of the superorder Hoplocarida presented in this paper is based on the new evidence contained in the Middle Pennsylvanian forms described above. All of the characters listed above must be considered primitive in the hoplocarids. The enlarged abdomen and shortened thorax are related to the location of organs in the abdomen normally confined to the thorax, *i.e.*, the gonads, digestive caeca, respiratory organs, as well as the developed muscular system. The thorax becomes restricted to sensory and food-gathering functions. The three flagella of the first antenna are an enigma. It is difficult to explain why there are three antennular flagella instead of two as there are in other Malacostraca, and indeed why there are usually two instead of one as in other crustacea. The pereiopodal protopods have three segments instead of two, which Siewing (in Whittington and Rolfe, 1963, p. 100) thinks may be primitive. It is possible that the existence of three flagella and three protopodal segments may be due to a chance occurrence, *i.e.*, the ancestral hoplocarid possessed *these* two characters out of an array of possible variations on them. The general caridoid, on the other hand, had two flagella and two protopodal segments. Pleopodal gills are not secondary as some workers assumed. Siewing was correct in his assertion. The burrowing decapod *Callianidea* and the isopod *Bathynomus* have been said to have pleomeric "gills" but these are in fact modified setae, not primary structures derived from epipodites (fig. 139). The location of gills on the abdomen cannot be explained. In the caridoids the important organ systems are restricted to the thorax. The location of the gills thus results from a "primeval decision" as to which tagma to "perfect."

We can now assemble a probable history for the hoplocarids, taking into account the new Middle Pennsylvanian material (fig. 140). The earliest hoplocarid must have been similar to the aeschronectids.

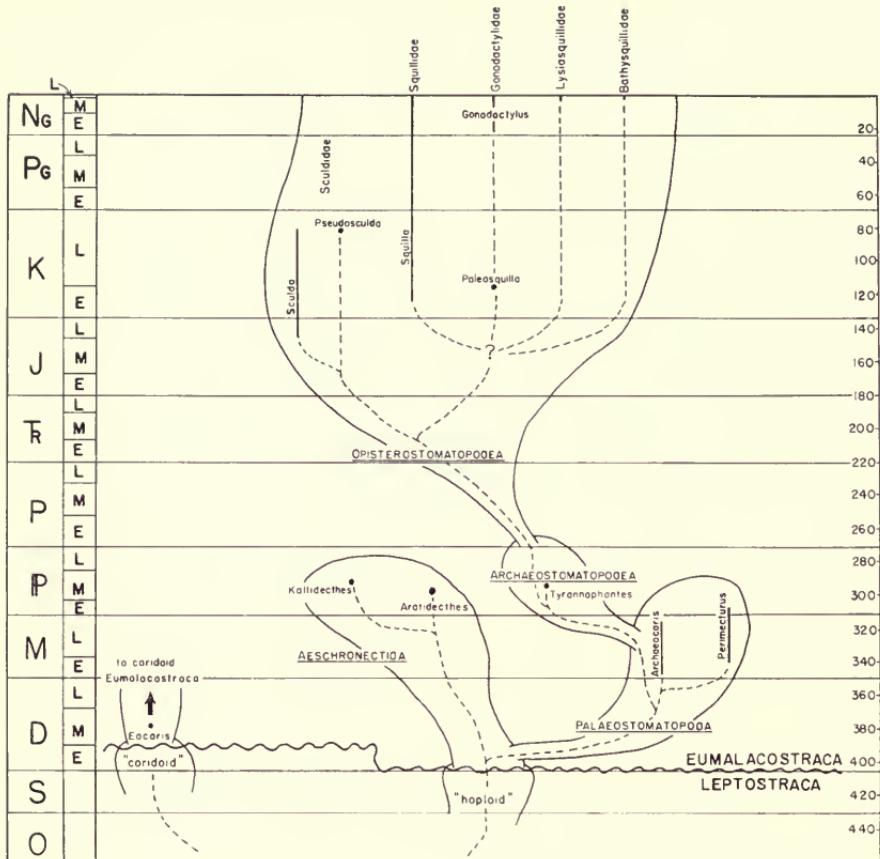


FIG. 140. The phylogenetic interpretation of hoplocarid relationships advanced in this paper.

The carapace covered the thorax, the thoracopods were not modified for food capture, and the gills were developed from protopodal epipodites. These animals were detritus or filter feeders, nektonic in habit. Certainly no later than the Early Mississippian the rapacious line, the palaeostomatopods, began to develop. Thoracic regionalization was initiated, the thoracic appendages became specialized, and the gills may have begun their relocation from the protopods to the exopods. The original nektonic forms persisted and gave rise to the aeschronectids. There undoubtedly were other non-rapacious hoplocarid types which have not yet been found as fossils. There is no reason to suppose that the Hoplocarida did not undergo an extensive radiation in the Middle and Late Paleozoic (perhaps well underway by the time the caridoids apparently initiated their radiation in the

Middle Devonian). The ancient hoplocarid carnivores became modified at the beginning of the Pennsylvanian in order to more efficiently employ their rapacious specializations. The carpus was reduced to facilitate thoracopod flexion and movement of prey to the mouth parts. The anterior thoracic segments became further reduced, moving the subchelate appendages farther forward for more efficient food handling. The modification of the tail fan was begun. Probably by Permo-Triassic time the opisterostomatopod level of organization was reached: the anterior thorax had been modified for maximum efficiency in food procuring and handling, the extreme specialization of the second thoracopod was well underway by that time, and the tail fan was perfected to the type familiar in the later fossil and modern "mantis shrimp." Toward the end of the Paleozoic, the aeschronectids and other ancient hoplocarids probably became extinct, perhaps phased out by competition with the more efficiently designed caridoid types.

It seems necessary to modify old opinions as to the origin of the Hoplocarida and the relationships within the Malacostraca. Calman (1909) recognized a suite of characters which he called the "caridoid facies." *These characters delineated a common structural type* from which more specialized members of each superorder, excepting the Phyllocarida, diverged. These characters are: the carapace enveloping the thorax; the eyes stalked; the antennules biramous; the antennal exopod scale-like; the thoracic appendages with a two-segmented protopod (coxa and basis), natatory exopods, *i.e.*, a flagelliform, setiferous structure, and a five-segmented endopod (ischium, merus, carpus, propodus, and dactylus); the abdomen slightly flexed and consisting of six segments (from embryologic evidence it appears that the primitive extra seventh segment is lost at the distal end); the tail fan formed by lamellar uropodal rami spread out on either side of the telson.

In addition to the above characters, there are others which are true of all Malacostraca. The trunk is sharply divided into thoracic and abdominal tagmata. These tagmata contain a fixed number of segments; eight in the thorax, primitively seven in the abdomen. The female genital pore is on the sixth thoracomere, while the male genital opening is on the eighth. The phyletic explanation attached to all the above mentioned characters has come to be known as the caridoid theory.

The hoplocarids differ in *some* of the items under the caridoid facies. They bear a number of similarities to the leptostracans. An

opposing array of characters might be listed, contrasting to the caridoid facies (for convenience, termed here the "haploid facies"). These characters elucidate a generalized morphotype from which the advanced hoplocarids diverged. These characters are: the carapace covering the entire thorax; the cephalon divided by a kinesis into an anterior procephalon bearing the stalked compound eyes and tri-flagellate first antennae, and a postcephalon; the rostrum movably articulated; thoracopods primitively all alike with a three-segmented protopod (preoxa, coxa, and basis), a one-segmented outer branch, and a four-segmented inner branch (ischio-merus, carpus, propodus, and dactylus); the abdomen very enlarged, containing the bulk of the gonads, digestive caeca, heart, respiratory organs, in addition to the muscles of the abdomen; the telson styloid with caudal furcae and the uropods blade-like.

There appear to be some problems in reconciling certain aspects of the haploid facies with the caridoid facies. The earliest caridoids (closely conforming to the caridoid plan) are known from the Middle Devonian. It appears that the hoplocarids must have been a distinct line from at least the Middle Devonian, if not earlier, since the earliest hoplocarids in the earliest Mississippian (*Archaeocaris vermiciformis*) are already quite specialized and divergent from what the ancestral type was like. The time allotted, within our present understanding of the fossil record, to derive the primeval haploid morphotype from the generalized caridoid is quite short. Of course, Silurian or Ordovician Eumalacostraca may be found.

The vast reorientation of the entire trunk which would occur due to the relocation of the gills from the thoracopods to the pleopods is difficult to envision. Thoracopodal epipodite gills had to be lost and replaced by pleopodal epipodite gills. Such a change on the part of a caridoid would require changes in the anatomy of the circulatory system and circulatory patterns within the body, modifications of the various organ systems for optimal accommodation to the new patterns, abandoning of former locomotory behavior, and rechanneling of currents around the body because of the new location of the gills.

The well-developed kinesis which exists in the hoplocarids (and leptostracans) would have to be perfected through the intermediary of a non-kinetic caridoid condition. A kinesis of sorts is recognized in some higher Eumalacostraca; however, it is not nearly as well developed as that in the leptostracans and the stomatopods. The loss of such a mobile area with its associated muscles in the caridoids and

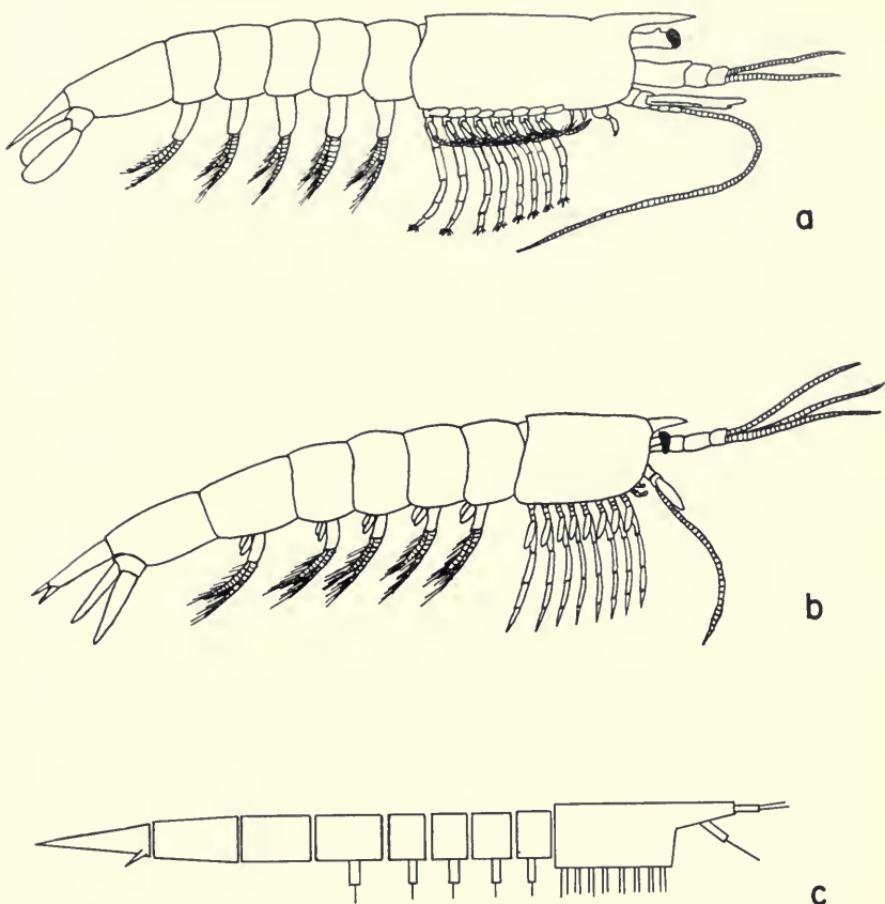


FIG. 141. a. Generalized caridoid from Calman (1909); b. generalized hoploid deduced in this paper; c. morphotypic rendition of parts of the unnamed leptostracan from the Essex fauna which offers some analogies to the generalized hoploid type.

then re-evolving of this system in the hoplocarids is contrary to evolutionary patterns.

It thus seems quite possible that the Hoplocarida arose independently from somewhere within the Leptostraca. The Eumalacostraca, as currently understood, are then to be considered polyphyletic with at least two independent lines, the hoplocarids and the "caridoids."

Brooks (in Whittington and Rolfe, 1963, p. 162) hesitated to suggest an independent origin of the hoplocarids because of a lack of a suitable ancestor within the leptostracans. There now appear to be some Leptostraca which do not conform to a nebulacean plan and

are hoplocarid-like. There is an as yet undescribed form from the Essex fauna which is apparently related to *Sairocaris elongata* (Peach, 1883) as most recently reconstructed by Rolfe (1969). A schematic morphotypic rendition of this animal is offered in Figure 141. Some points of agreement between the hoploid facies and this morphotype are evident. These are: a definite preoral area of considerable size and an arrangement of structures as in the aeschronectids suggesting a kinesis; the carapace covering most of the thorax; the thorax markedly reduced in relation to the abdomen; the posterior abdominal somites elongate with the anterior ones relatively shortened. It thus not only seems logical to admit the possibility of an independent origin of the hoplocarids, but the fossil record of the leptostracans, poorly understood as it is, might provide us with a possible ancestral analog. We cannot insist all Leptostraca were like the Nebaliacea.

Manton (in Whittington and Rolfe, 1963, p. 139; 1964) has strongly supported the *probability* of extensive polyphyly within the Arthropoda. (By polyphyly she accepts the definition of Kermack and Mussett (1959) that a group is polyphyletic if the immediate ancestor of the members of that group would not itself be a member of that group.) Brooks (in Whittington and Rolfe, 1963, p. 161) believed the Malacostraca were probably polyphyletic. J. T. Woods (1965) did not disregard the possibility of the Eumalacostraca being polyphyletic, observing that similarity in developmental grades in independent lines of early phyllocarids would be difficult to detect in the later Paleozoic Eumalacostraca.

Olson (1959) developed some concepts which might be applied to the supposed early history of Malacostraca. The transition from the primordial malacostracan ancestor, possibly a cephalocarid, to what corresponds to a malacostracan grade was gradual. During this time one group may have placed a morphotypic emphasis on the thorax, leading eventually to the general "caridoid" line; another line would have developed the abdomen, leading to the "hoploid" type. Both these groups would have continued to evolve through the leptostracan grade of organization. Eventually the "caridoid" and "hoploid" types would have reached the threshold that delineated the eumalacostracan grade of organization. There would be common characters in these leptostracan lines which would be more fully expressed in their later history.

This proposition of polyphyly is not meant to disregard the possibility of monophyly. Some arguments for monophyly can be ad-

vanced. The primitive caridoid cephalon may have been kinetic, the mobility of the head region being lost as the caridoid line evolved. This is quite possible in view of the fact that what we know of the leptostracans would indicate that a cephalic kinesis is the rule in phyllocarids. Consequently, the caridoid would have had a cephalic kinesis sometime in its history. The other alternative, which was mentioned above, is that the haploid kinesis would have evolved from the primitive nonkinetic caridoid cephalon before the rostrum became fused. This implies that, leptostracans having had a mobile cephalon, the kinesis was lost in the caridoid and then re-evolved in the haploid. This is contrary to all evolutionary patterns and is decidedly complicated and, using Occam's razor, to be queried if a simpler explanation offers itself.

The implied inadequacy of time in evolving a haploid from a caridoid may not be an argument at all. Though we do not have eumalacostracans before the Middle Devonian this does not mean that there were none. Until some eumalacostracans are found, however, in the Silurian or Ordovician we must work with what we have. The fossils known are very primitive caridoids, so we might assume that the previous step in that evolutionary sequence was a leptostracan.

One might also argue that the relocation of the gills on the pleopods may not be a difficulty. Other groups have independently evolved "gills" on the abdomen; the callianassid mentioned above, *Callianidea*, modified the pleopodal setae; the isopods employ the entire abdominal appendage. No other groups have such well developed pleopodal epipodite gills, however, as the hoplocarids. The evolution of branchial structures on the pleopods of the aeschronectids and stomatopods is not at all comparable, in my opinion, with the modification for respiration of existing structures in the isopods and decapods. The loss of thoracopod epipodite gills and the evolution of pleopod epipodite gills is much more difficult to envision than is the loss of the gills and the mere modification of an existing structure. Thoracic epipodite gills and abdominal epipodite gills reflect, to me, entirely different orientations, a basic dichotomy in tagmatic organization. It is difficult to see how or why this reversal of orientation took place. A simpler explanation would be a "neutral condition" in the leptostracans (or maybe preleptostracans) from which, over a long period of time, one line organized its internal anatomy around the thorax (leading to the caridoids) and another line organized its internal anatomy around the abdomen (leading to the haploids).

Between the hoploid and caridoid facies certain points of similarity emerge which may reflect basic relationship, such as a scale on the second antenna, and uropods with the complex abdominal musculature. These characters within the framework of the caridoid theory are unique and form a strong argument for monophyly in the Eumalacostraca. Such a system as the complex abdominal musculature would be the basis of a very strong argument (Hessler, 1964); such a specialized system as this in the Eumalacostraca may have only evolved once. But, in light of Manton's (1964) arguments on the convergence in mandibles, compound eyes, and spiracular gills, these points may not be as conclusive as they would first seem. If compound eyes, complex as they are, are convergent and if we accept the fact that there are certain optimal ways in which certain functions can be performed, then the possibility of convergence in the abdominal musculature and uropods, and seaphocerites cannot be ruled out. Moreover, although there is an apparent anatomical similarity in the abdominal musculature of caridoids and the stomatopods, there is no similarity in function. Stomatopods do not possess the caridoid escape reaction which is associated with these muscles. Mantis shrimp will roll over, flip over, or turn around when startled, but they will never swim backward. The uropods are not used for swimming but are employed as stilts along with the posterior thoracic appendages in keeping the body, especially the abdomen and its gills, above the substrate.

There remains the interpretation of Siewing (1956) that it is the first abdominal segment of the primitive leptostracan condition of seven that was lost in the Hoplocarida. If this is true, then there is indeed a basic difference between the hoploids and the caridoids who lost the last abdominal segment. We must remember that we have only the anatomical evidence in the adult stomatopods to support this claim. We cannot forget Shiino's (1942) apparently contradictory embryologic evidence of an extra set of myomeres and ganglia in the last segment.

The seemingly minor—minor because they have never been considered important in the past—anatomical differences are left to consider. These differences between hoploid and caridoid are: three protopodal segments in the thoracopods instead of two, three antennular flagella versus two, flap-like exopods as opposed to natatory exopods, and four segments in the endopod compared to five. Why these states exist cannot be determined. Perhaps the inability to explain these differences away is important to the case for polyphyly. These character states may be due to chance. They do

not occur erratically throughout both lines. This may indicate that they arose once, thus imparting unity within the caridoids and hoploids and delineating a separation between the two.

I have suggested therefore that in light of the evidence at hand the Eumalacostraca may be polyphyletic. One must concede that strong arguments can be made for monophyly. However, it appears an assumption of an independent origin for the Hoplocarida is a simpler position to maintain. There is also some evidence in the loss of the first abdominal segment and this is very difficult to explain by monophyly. Some points which might be considered minor anatomical evidence emphasize the separateness of hoploid and caridoid lines.

The controversy resolves itself into attempting to move the hoploids close to the caridoids and in determining where to draw the line between Leptostraca and Eumalacostraca. I do not believe we can bring the two lines together as we now understand them, although alternative explanations can be made and future evidence may strengthen or weaken the arguments. Where and when leptostracans gave rise to eumalacostracans must remain an open question for the time being. It appears that the hoploids and caridoids are far enough apart morphologically so that a common ancestor lies within the Leptostraca.

If the Eumalacostraca are polyphyletic, what would be the status of the term *Eumalacostraca*? Simpson (1959) enumerated some taxonomic principles which may be adopted here. First, Eumalacostraca may be defined as a *grade* of morphologic organization. Second, Eumalacostraca might be restricted to groups suspected of being monophyletic, *i.e.*, descended from a "caridoid" ancestor (Eocarida, Peracarida, Pancarida, Eucarida, and possibly the Syncarida). Third, retain Eumalacostraca as a polyphyletic division. Simpson claims that it should be a sufficient principle of evolutionary taxonomy that each taxon arose wholly from one of lower categorical level. It should be pointed out that we cannot be sure whether the *series* Eumalacostraca can be derived from a superorder, *i.e.*, how uniform a group are the phyllocarids? Can the Phyllocarida easily encompass the "caridoid" and "hoploid" types? Fourth, one could expand the definition of the Eumalacostraca to include the common ancestor of both the caridoid and hoploid types. This expansion, however, could well permeate all the way back to the cephalocarids. It seems that it is pragmatic to maintain alternative three for the time being, though alternative one seems the more preferable.

SUMMARY

Three new Middle Pennsylvanian Hoplocarida are described which significantly expand our knowledge of the hoplocarid radiation. Modification and expansion of the definitions of the higher taxonomic levels of the superorder are presented. A short history of phylogenetic speculation on the hoplocarids is offered along with some additional considerations in light of the new material. An archetypal hoplocarid is proposed which seems to find an analog in some leptostracan forms. The polyphyletic nature of the Eumalacostraca and some ramifications thereof are considered.

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